

An integrated age- and length-structured population model for snapper with a simulation comparison of a conventional age-structured model

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7. Executive Summary

This report describes some new developments in fish population modelling which have particular relevance to New Zealand snapper. We have developed a population dynamics model of the Catch at Age and LENgth (CALEN) that describes the stock by numbers of fish in an age×length matrix similar to that of Guldbrandsen Frøysa et al. (2002). Fish growth is defined by functions of length and sea surface temperature. Between-fish and between-year growth variations are modelled. This report updates the previously reported results of project SNA1999/01 by providing the final results of the model development in three sections: a description of the length-based parametric growth function, a description of the model and the fit to the Hauraki Gulf/Bay of Plenty snapper data, and a comparison between CALEN and the conventional Age-structured MODel (AMOD). The three separate sections are attached as draft manuscripts; each forming a part of the Final Research Report, and each prepared for submission to a scientific journal.

We have developed functional forms for growth that best fitted Hauraki Gulf/Bay of Plenty (New Zealand) snapper (*Pagrus auratus*) population data. Growth was estimated that includes between-year and between-fish variability. Both length- and age-length-dependent growth processes were required to explain the data. For each age-length cell of the population matrix, there is a transition vector that determines the proportions that grow 0, 1, 2... cm. Growth is Markovian in the sense that it is determined only by the current state. The growth increments followed a truncated lognormal distribution. The mean increment for each cell was primarily an exponential function of length. There was a small age-length effect consistent with phenotypic plasticity, which tended to continue the unusual growth of individuals that were already "stunted" or "giant", without assuming any genetic effect. There was also an annual environmental effect that multiplicatively modified the mean increments. This effect was positively related to sea surface temperature. There was a large stepwise increase in growth variability that occurred at about the length of maturity and appears to arise from individual "choice" between growth and reproduction. Such an effect may not have been previously modelled. The CALEN model accommodates these relationships.

The data that we fitted CALEN to were: commercial and research estimates of proportions at age and length, commercial estimates of proportions at age, tagrecapture estimates of numbers by length class, and a catch per unit effort relative abundance index, together with sea surface temperature data. Annual mean growth and annual year class strength were both found to be positively related to sea surface temperature, but during different seasons. We found that apparently modest variations in annual growth resulted in substantial and sustained fluctuations in population biomass. We were able to investigate the effects of potential length-based management controls.

Biomass and yield estimates derived using a Catch at Age-LENgth-structured model (CALEN), with length-based, and temperature-dependent, growth and recruitment processes, (Gilbert et al. this report, section b) fitted to New Zealand snapper data were compared with those from a conventional Age-structured MODel (AMOD) that assumes constant annual growth. AMOD constant mean weight at age differed markedly from CALEN estimates that reflected the cumulative effects on cohort length frequencies of temperature-dependent growth during a cool El Niño period, length-based fishing mortality, and year class strength variability. AMOD annual biomass estimates were consistently higher than CALEN. Bias and variance in these estimates was calculated from parametric bootstraps conditioned on CALEN as a "true" population. Under the structural and error model assumptions made for the "true" population, AMOD bootstrap estimates of snapper stock biomass and status were highly positively biased. The results suggest that model uncertainty estimation conditioned upon structural model assumptions regarding growth variability is an important element in fish population studies. New Zealand sea temperatures are largely determined by El Niño Southern Oscillations, so temperature-driven growth variability, and its recruitment effects, has significance for assessing and managing snapper. This may also be true for other temperate stocks exhibiting these features.

8. Objectives

This project has an overall objective that relates to the medium term research strategy for snapper as follows.

1. To carry out stock assessment of snapper (*Pagrus auratus*), including estimating biomass and sustainable yields.

The specific objectives of the project as carried out in 2001/2002 have been modified since the implementation of the project in October 2001 by means of two contract variations, which added specific objectives 3 and 4.

Specific Objectives:

- 1. To update the CPUE analyses for SNA 1 and 8 using data up to the end of 1999/2000.
- 2. To update the assessment of snapper stocks SNA 2 and 7.
- 3. To develop an integrated age-length model.
- 4. To prepare and read otolith samples from Kaharoa surveys KAH8810 and KAH0012

The specific objectives 1 and 4 have been completed with the submission to the Ministry of Fisheries of two separate Final Research Reports, and specific objective 2 by the submission of a draft Fisheries Assessment Report. This report (presented here in 3 sections) completes specific objective 3.

The submission of this final research report achieves the revised final reporting requirement for SNA2000/01.

For sections 9 through 14 see the attached 3 reports.

9. Introduction

10. Methods

11. Results

12. Discussion and Conclusions

13. References

14. Appendix

15. Publications

No publications have been finalised during this project, however a draft FAR was produced for objective 2, and we hope that sections a, b, and c of this FRR for objective 3 will be approved for submission to a scientific journal.

16. Data Storage

No new data was collected during this project.

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Section a

Gilbert, D.J., Davies, N.M., and McKenzie, J.R. (In prep.) A growth model for snapper (*Pagrus auratus*) with between-year and between-fish variability. *Marine and Freshwater Research*.

Abstract

We describe a stochastic model for annual fish growth. It was developed within a population model in which the population state is a numbers-at-age and centimetre length-class matrix. Gilbert et al. (this issue b) fitted the model to data from the Hauraki Gulf/Bay of Plenty (New Zealand) snapper (Pagrus auratus) stock. For each age-length cell of the matrix there is a transition vector that determines the proportions that grow 0, 1, 2... cm. Growth is Markovian in the sense that it is determined only by current state. The growth increments follow a truncated lognormal distribution. The mean increment for each cell is primarily an exponential function of length. There is a small age-length effect consistent with phenotypic plasticity, which tends to continue the unusual growth of individuals that are already "stunted" or "giant", without assuming any intrinsic differences between fish. There is also an annual environmental effect that multiplicatively modifies the mean increments. This effect is positively related to sea surface temperature. There is a large stepwise increase in growth variability that occurs at about the length of maturity and appears to arise from individual "choice" between growth and reproduction. Such an effect may not have been previously modelled.

Introduction

Conventional age-structured population models typically assume that fish growth is a constant function of age (Hilborn and Walters 1992). For stock assessment purposes this may be an undesirable oversimplification. A model with between-year growth variability will include changes in the mean weights at age from year to year and changes in the relative proportions of the youngest age-classes that have recruited to the fishery. It may estimate a substantially different population biomass trajectory and perform better than a model that does not capture these processes, especially where both models are fitted to abundance indices. It is difficult to satisfactorily account for between-year variability in growth using an age-structured model. Such models must also approximate size-dependent processes by age-dependent ones and are therefore unable to carry forward the effects of a deviation from mean growth in a particular year (Parma and Deriso 1990). Nor can they adequately carry forward lengthdifferential fishing effects or the effects of size-based management controls such as size limits. To address these shortcomings there have been several approaches to developing population models that carry both age and length structure (Guldbrandsen Frøysa et al. 2002, Punt et al. 2001, Parma and Deriso 1990)

Between-year growth variability in commercial fish species is well documented in the literature (Brander 2000, Ottersen and Loeng 2000, Cardinale and Modin 1999, Clark et al. 1999, Shelton et al. 1999, Campana 1996, Campana et al. 1995, Francis et al. 1992, Mehl and Sunnanå 1991) and has usually been attributed to environmental effects. Millar et al. (1999) showed that sea surface temperature (SST) was a good

predictor of annual growth for Hauraki Gulf/Bay of Plenty snapper. The dataset they used was a subset of that used here and we confirmed their result.

In this paper we describe a stochastic model for annual fish growth that was developed as a component of the population model described by Gilbert et al. (this issue b). A third related paper is a comparison between estimates from the population model and an age-structured model (Davies et al. this issue c). The population model was developed to enable the assessment of the Hauraki Gulf/Bay of Plenty part of SNA 1, the snapper (Pagrus auratus) stock occurring in the northeast of the North Island of New Zealand. It employs a matrix of numbers-at-age and centimetre lengthclass to represent the annual state of the snapper population (Guldbrandsen Frøysa et al. 2002). The growth model allows fish growth to vary between years and between fish. For each age-length cell of the matrix there is a transition vector that determines growth. There is no negative growth. Growth is Markovian in the sense that the transition vector is determined only by age, length and a year effect. The year effects may optionally be related to an exogenous environmental variable. The model does not have groups or cohorts of fish with intrinsically different growth. The population model was fitted by maximum likelihood to commercial and research age-length samples collected over 25 years, as well as to abundance estimates. Gilbert et al. (this issue b) describe the data and the fitting process. Here we describe only the growth model.

Growth model

We model growth by determining the proportions of fish in a particular age-length cell, in a particular year, that grow 0, 1, 2... cm. Mean growth increment is primarily a function of length (described by 3 parameters). There is also a small age-length effect (2 parameters). Mean increments vary between years by an annual, multiplicative factor that applies to all cells of the matrix (1 parameter per year). These factors are related to SST during winter. Hence, as an alternative model, they can be replaced by an SST predictor (1 parameter). The model explained the data parsimoniously (see Gilbert et al. this issue b). The standard deviation variable that determines variability around each mean increment is a function of the mean and has a stepwise change at about the length of maturity (4 parameters). We integrate a truncated probability density function into 1 cm steps to determine the proportions that grow into each new age-length cell.

Mean increment function

For many fish species the von Bertalanffy function describes mean length at age well. By subtracting length functions for successive years, the increment can be shown to be a linear function of length. A linear function is therefore a useful starting point in a search for an equation for mean growth increment. If l is fish length, then the expected growth increment,

where $-1 < \alpha < 0$ and $\beta > 0$. The parameters can be expressed in terms of the von Bertalanffy parameters, k and L_{∞} , by $\alpha = -(1 - e^{-k})$ and $\beta = L_{\infty}(1 - e^{-k})$. Instead we used the parameterisation of Francis (1988),

where the parameters μ_{10} and μ_{30} are the growth increments that would occur at lengths 10 and 30 cm: $\mu_{10} > 0$ and $\mu_{10} > \mu_{30}$. The lengths 10 and 30 cm are suitable for snapper, but otherwise arbitrary. Estimates of μ_{10} and μ_{30} tend to be uncorrelated, unlike the parameters k and L_{∞} , or α and β . Estimating μ_{10} and μ_{30} is therefore more satisfactory. Also, these parameters can be used in other growth functions while retaining their meaning.

As expected, Equation (2) fitted the data reasonably well. It did not, however, provide the best fit. Where $l = \frac{30\mu_{10} - 10\mu_{30}}{\mu_{10} - \mu_{30}}$ the function meets the x-axis and growth ceases,

i.e., $l = L_{\infty}$. Beyond this length mean growth is negative (Fig. 1). Below we test the normal distribution to describe growth increments around the mean. Negative increments in the distribution can be lumped at zero. Lumping ensures that the effective mean increment becomes positive or zero at all lengths. However Equation (2) provided an unsatisfactory fit to both the youngest and oldest fish. We therefore sought a function that approached zero asymptotically. The function proposed by Deriso and Parma (1988) was rejected because it also fell to zero at a finite length. A three-parameter "hockey stick" function described by Cranfield et al. (1996), which is linear but has an appended asymptotic curve at the right hand end, did not fit the data well. Neither did the function proposed by Guldbrandsen Frøysa et al. (2002) and used by Millar et al. (1999) where growth increment was proportional to a power of the reciprocal of length. We added a third parameter to make the function a power of the reciprocal of length plus an offset, but this still did not fit the data well. The best fit was obtained using an exponential function of length that can be expressed,

where $\mu_{10} > \mu_{30} > 0$ (Fig. 1). Our model estimates were $\hat{\mu}_{10} = 6.72$ cm and $\hat{\mu}_{30} = 3.23$ cm.

The parameter l_0 , the length at age 0 y, is required to fully define growth. Mean growth is thus defined by 3 parameters. Our model estimate was $\hat{l}_0 = 2.5$ cm. Hence all fish entering the population at age 0 y are in the 2–3 cm length class. Since our samples did not contain fish at age 0 y, our estimate of l_0 was simply a value that generated the right lengths at age 1 y. Under these circumstances, the parameter l_0 is like the von Bertalanffy parameter t_0 , it does not necessarily have a realistic interpretation. Others have assumed that a cohort entering the stock occupies a range of lengths, but this is often at an age greater than 0 y. We found that a further parameter allowing 0-year-old fish to enter the population by way of a distribution of lengths around l_0 did not significantly improve the fit.

Annual growth factor

Like Millar et al. (1999) we found monthly mean SST's to be a significant predictor of mean growth. We did not search every combination of months, but amongst 6-monthly SST means the period April–September gave the best predictors. The best model was a linear factor, independent of length, which multiplied the mean growth increment. If T_y is the SST deviation from mean SST, then the mean growth increment at a particular length is given by,

where the parameter $\gamma_{0.5}$ equals the growth factor that would apply when $T_y = 0.5^{\circ}$ C. Our model estimated a positively sloped relationship: $\hat{\gamma}_{0.5} = 1.057 \,^{\circ}$ C⁻¹. Although this function is unbounded and takes negative values, we found that the fitted values remained positive and within a feasible range. Domed and sigmoid functions were tried but these did not fit the data as well as Equation (4).

While this function significantly improved the model fit, it is clear that in some years SST systematically under- or over-estimates growth. We therefore fitted an alternative model with individual annual growth factor parameters.

This model gave a significant improvement to the fit. Because the minimiser we were using was only able to fit a maximum of 50 parameters (Gilbert *et al.* this issue b), we fitted annual growth factors for 1991–2000, where data were good, and used the SST-based factors elsewhere (Fig. 2).

Age-length effect

The model described so far failed to satisfactorily fit the growth of a few "stunted" or "giant" fish. We made a modest improvement with a factor that depended on how much a fish's length differed from the mean length at its age i.e., an age-length-dependent function. The factor made fish that had got ahead of their cohort tend to continue to grow faster than their equal sized, older peers, and conversely. The inverse tangent function that constrains the factor within bounds and is symmetric around zero was found to fit well. The mean growth increment for a fish of length l, age a, is multiplied by the factor,

where the parameter $\phi_{1.5}$ equals the factor that would apply if a fish were 1.5 times the mean length for its age and ϕ_{∞} equals the asymptotic factor: $0 \le \phi_{\infty}, \le 2$. The factor, ϕ , is constrained to be within the range $(2-\phi_{\infty}, \phi_{\infty})$. Our model estimates were $\hat{\phi}_{1.5} = 1.18$ and $\hat{\phi}_{\infty} = 1.46$. The mean length at age is calculated by successively adding mean annual increments. The mean length at age 1 y,

$$\overline{l_1} = l_0 + \left(\frac{\mu_{30}}{\mu_{10}}\right)^{l_0/20} \cdot \frac{\mu_{10}^{\gamma_2}}{\mu_{30}^{\gamma_2}}$$

Fig. 3 shows how the age-dependent function varies above or below one, as fish length varies above or below the mean length at age. The full expression for the mean growth increment for a fish of length l and age a in year y is,

$$\mu_{lay}' = \left\{ 1 + \frac{2}{\pi} \left(\phi_{\infty} - 1 \right) \tan^{-1} \left[2 \tan \left[\frac{\pi}{2} \left(\frac{\phi_{1.5} - 1}{\phi_{\infty} - 1} \right) \right] \cdot \left(\frac{l}{\overline{l_a}} - 1 \right) \right] \right\} \cdot \left\{ 1 + 2(\gamma_{0.5} - 1)T_y \right\} \cdot \left(\frac{\mu_{30}}{\mu_{10}} \right)^{\frac{l}{20}} \cdot \frac{\mu_{10}^{\frac{\gamma_2}{\gamma_3}}}{\mu_{30}^{\frac{\gamma_2}{\gamma_3}}}$$
(8)

where the factor in the second braces may alternatively be replaced by g_{y} .

Individual variability

Guldbrandsen Frøysa et al. (2002) propose both parametric and non-parametric approaches to obtaining a distribution of growth increments from an age-length cell. We use a parametric approach. Deriso and Parma (1988) suggest that distributions of length at age usually show positive skewness and the data used here support this observation (see Fig. 4). The model fitted well when growth increments were distributed lognormally. The positive skewness in the lognormal increments translates to positive skewness in the distributions of length at age from about age 4 y onwards. To obtain a good fit to the data it was necessary to make the standard deviation of the increments a function of both mean increment and length, according to four parameters, ς_1 , ς_2 , ψ , and l^* . Standard deviation decreased somewhat with decreasing mean increment, governed by the parameter, ψ . The observed age-length distributions showed an increase in spread that occurred around ages 5 to 7 y and lengths 20 to 25 cm (Fig. 4). We model this to be dependent on length. A stepwise increase in individual growth variability at a specified length, l^* , significantly improved the model fit when l^* took values between 20 and 25 cm. The length increment standard deviation deviation parameter is,

$$\sigma_{l} = \begin{cases} \varsigma_{1} \left(\mu_{lay}^{\prime} \right)^{\psi} & \text{where } l < l^{*} \\ \varsigma_{2} \left(\mu_{lay}^{\prime} \right)^{\psi} & \text{where } l \ge l^{*} \end{cases}$$
(9)

The probability density for growth increment Δl , for fish of length l and age a, in year y,

$$f(\Delta l) = \frac{1}{\sqrt{2\pi}\sigma_l \Delta l} \exp\left[-\frac{1}{2} \left(\frac{\log(\Delta l) - \log(\mu_{loy}') + \frac{1}{2}\sigma_l^2}{\sigma_l}\right)^2\right].$$
(10)

The function $f(\Delta I)$ is integrated in 1 cm segments to give the transition proportions (Fig. 5). We set a maximum length class of 70–71 cm and fish in this cell do not grow. The data showed fish longer than 70 cm to be extremely rare. The integral from 0 to 0.5 cm gives the proportion that remain in the same length cell, that from 0.5 to 1.5 cm gives the proportion that grow to the next length cell, etc. The right hand tail of the distribution is truncated to remove transition proportions that are less than 0.005 and the remaining proportions are rescaled to sum to one.

and

Our model estimates were $\hat{\zeta}_1 = 0.59$, $\hat{\zeta}_1 = 2.05$, $\hat{\psi} = -0.45$ and $l^* = 22$ cm. Fig. 4 shows the fit to two selected age-length samples (out of 37). The modelled catches are taken via gear-specific selectivity curves. The downward kink in the length at age curve at ages 9 and 10 y corresponds to a period of slow growth in the cold years 1992–94, when these cohorts were juveniles. The model fitted the increasing spread of length at age above length 22 cm. The differences between trawl and long-line mean lengths at age are caused by selectivity differences.

Whereas discretisation has a minor effect on mean growth, the treatment of the tails of the growth distribution causes the effective mean increment for age a, length l and year y to differ from μ'_{lay} . Growth less than 0.5 cm is treated as nil growth and the right hand tail is truncated. When $l \ge l^*$, σ_l is relatively large and the right hand tail is relatively long. The truncation causes the effective mean increment to be considerably smaller than μ'_{lay} (Fig. 6). These effects are cumulative, causing the modelled mean length for large a to be substantially less than \overline{l}_a . The effective mean increment at l = 30 cm predicted by the model is 2.34 cm even though the parameter estimate $\hat{\mu}_{30}=3.23$ cm (Fig. 6). This is largely a theoretical problem since data is fitted to the effective mean increment. However the step in the mean increment curve at 22 cm is not entirely plausible. We did not test alternative truncation rules for the right hand tail of $f(\Delta l)$. We also did not test whether the age-length effect would fit the data better with \overline{l}_a replaced by the effective mean increment.

A normal distribution with the left-hand tail lumped at zero was tested as a possible alternative model for individual growth variability, but fitted the data less well, probably because of its failure to replicate the positive skewness. In this case, each effective mean increment for age *a*, length *l* and year *y* also differs from μ'_{lay} . Again the greatest differences occur for large *a*. Here the effect of lumping the left hand tail of the distribution at zero predominated over truncation of the right hand tail. While $\hat{\mu}_{30}$ =1.97 cm, the effective mean increment at *l* = 30 cm was again 2.34 cm.

Discussion

None of the parametric functions for growth that have been described elsewhere was found to provide a good fit to the Hauraki Gulf/Bay of Plenty snapper age-length data. We do not know whether the functional forms that were successful here would prove to be best for other fish populations. We believe that they may be, but we emphasise that the acid test in each case would be the quality of the fit to the data.

We found that a two-parameter exponential function of length could satisfactorily model mean annual growth increment. Various functions that have been proposed elsewhere (Guldbrandsen Frøysa et al. 2002, Millar et al. 1999, Deriso and Parma 1988, Cranfield et al. 1996) were either less satisfactory at the youngest ages or at the largest lengths, even when they utilised more than two parameters. An improved fit was obtained when the exponential function was modified by an annual multiplicative factor (taking values between 0.7 and 1.2) that was related to SST in a manner consistent with the results of Millar et al. (1999).

The fit was further improved by an age-length factor that was a function of the ratio of a fish's length to the expected length for its age. The factor causes fish that have got ahead of their cohort to tend to grow faster than their equal sized, older peers, and conversely. It is not a genetic effect involving intrinsic differences between fish. The effect is Markovian in the sense that growth is determined only by the current state. The age-length factor was nevertheless able to improve the fit to the few stunted or giant fish in the samples. Our result allows the possibility that phenotypic plasticity is a sufficient explanation for extremes of growth variability. We are not aware of a growth model of this type having been described before. We did not test genetic models involving intrinsic growth variability between fish in a cohort or between cohorts. We do not argue that a genetic model could not explain these data equally well; only that such a model cannot necessarily be inferred from data containing wide growth variability.

An unexpected result was the large stepwise increase in growth variability estimated to occur at 22 cm, although evidence for it can be seen in the research trawl agelength samples (e.g., Fig. 4). Crossland (1977) gives 23 cm as the length at which 50% of Hauraki Gulf snapper are mature. A possible explanation of the variability is that before maturity all surplus energy goes into growth, but after maturity fish have a 'choice' between putting energy into growth or into reproduction and there is a wide range of ways this choice is exercised. We are not aware that such an effect has previously been modelled.

The use of an unbounded distribution to model growth increments meant that it was necessary to truncate the right hand tail to avoid a tiny proportion of fish exhibiting unfeasibly large growth. This caused the means of the transition vectors to differ from the nominal means. It also caused an implausible step in the effective mean increment versus length relationship. Our truncation rule was to arbitrarily discard proportions less than 0.005. Guldbrandsen Frøysa et al. (2002) encountered difficulties employing non-parametric transition vectors and suggested the use of the discrete beta-binomial distribution instead. They truncated their distribution by arbitrarily fixing the maximum amount a fish could grow. It may be worthwhile to seek a growth distribution-truncation rule that fits the data better than those described above.

We have achieved a description of snapper growth that includes between-year and between-fish variability with 9 parameters plus one parameter per year. Within an age-length structured population model this allows both length- and age-dependent processes. The effects of length-dependent selectivity can be properly modelled, even when growth varies between years. The variable timing of the entry of cohorts into the recruited stock from year to year as growth varies, can be modelled. The accumulation of fish in a maximum-age group can be adopted without the need to assume constancy of mean length. The effects of length-based management measures such as size limits can be predicted (Gilbert et al. this issue b). The population model allows the better prediction of the consequences of both natural climate/environment variation and of fisheries management measures than is possible in an age- or a length-structured model.

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Fig. 1. Exponential and linear (equivalent to a von Bertalanffy function) models of annual mean growth increment as a function of fish length.



Fig. 2. Annual growth factors that multiplicatively modify mean growth for fish of all lengths. The triangles are predictions that are a function of winter sea surface temperature (SST) and the circles are independently estimated annual factors. Because the minimiser we were using was able to fit only 50 parameters we estimated growth factors for 1991–2000 and used the SST predictions up to 1990. The former suggest that the latter may systematically overestimate growth between 1991 and 2000.



Fig. 3. Growth factor contours based on an inverse tangent function of the ratio of length at age to mean length at age. For fish on the mean length at age line the mean growth increment is a function of length as in Fig. 1. On the long-dashed lines the mean growth increment is 5% greater or smaller than that predicted by length. Lines along which 10% and 15% effects occur are also shown. Note that these are not growth paths but rather contours showing the size of deviations from the purely length-dependent growth.



Fig. 4. Observed and fitted snapper growth model for research trawl and commercial long-line samples taken in 2001 from Hauraki Gulf, New Zealand. Areas of circles are proportional to numbers in catch. Curved heavy lines are fitted mean length at age. Light lines are estimated 5 and 95 percentiles of length at age. The horizontal line in the upper plot is the length at which there is a stepwise increase in growth variability. In the model, fish are accumulated at age 30 y (but continue to grow). The commercial minimum legal size is 25 cm.







Fig. 6. Mean annual growth increment at length calculated from a lognormal distribution (solid) showing the 5 and 95 percentile bounds for individual growth variability (dashed), and mean annual growth increment after discretisation and truncation (solid grey) with the minimum and maximum growth (dashed grey).

Section b

Gilbert, D.J., Davies N.M. and McKenzie, J.R. In prep. Application of an agelength structured model to the Hauraki Gulf/Bay of Plenty snapper population (*Pagrus auratus*). *Marine and Freshwater Research*.

Abstract

We have developed a population dynamics model that describes population state by a matrix of numbers at age and length. We have developed functional forms for processes that best fitted Hauraki Gulf/Bay of Plenty (New Zealand) snapper (Pagrus auratus) population data. For each age-length element of the state matrix, the model determines a transition vector that gives a distribution of non-negative growth increments. Growth includes between-year and between-fish variability. Both lengthand age-length-dependent growth processes were required to explain the data. Annual mean growth and annual year class strength were both found to be positively related to sea surface temperature, but during different seasons. Our model accommodates these relationships. We found that apparently modest variations in growth between years resulted in substantial and sustained fluctuations in population biomass. We were able to investigate the effects of potential length-based management controls. The data that we fitted the model to were: commercial and research estimates of proportions at age and length, commercial estimates of proportions at age, tagrecapture estimates of numbers by length class, and a catch per unit effort relative abundance index, together with sea surface temperature data.

Introduction

The simplest fish population dynamics models described population's state by a single number, its biomass (Pella and Tomlinson 1969, Schaefer 1954). More complex agestructured models were developed where population state was described by a vector of numbers at age (Gulland 1965). A considerable range of approaches to age-structured modelling evolved (Methot 1990, Deriso and Parma 1988, Deriso et al. 1985, Doubleday 1976). Where sufficient data existed these methods were able to model age-based processes well but could only approximate size-based processes. Sizestructured models where population state was described by a vector of numbers at length were also developed (Sullivan 1992, Schnute 1987, Jones 1981). These could model size- but not age-based processes, but in general performed less well than agestructured models because length-based data is typically less informative than agebased data. Size-based models tend to be used for species where ageing is difficult or impossible. The ongoing enhancements to available computing power have allowed increasingly complex models to be fitted and more recently age-structured models that contain multiple growth types have been developed (Punt et al. 2001). Here the population state is described by a matrix of numbers at age and growth type and hence size-based processes can be better approximated than for the simpler age-structured models. Guldbrandsen Frøysa et al. (2002) developed a model structured on both age and length where the population state is described by a matrix of numbers at age and length. We have developed a similar model in which population state is described in the same way. It allows both age- and size-based processes to be modelled with considerably fewer restrictive assumptions than the previous models.

In our model, recruitment and growth are random processes, so that the size of yearclasses entering the state matrix varies, as do the patterns of transition of year-classes through the matrix. Unlike for the simpler models, the effects on year-class length distributions of size-based processes such as fishing are fully retained in the state matrix. Because the effects on the population of age-, length-, and age-lengthdependent processes are retained, the effects of between-year growth variability on stock biomass can be modelled better than previously. The model deals naturally with variability in the proportions of an age-class that exceed minimum legal size (MLS) from year to year. The effects of length-based management measures can be predicted without recourse to age-based, constant size-structure approximations.

We model natural and fishing mortality as deterministic processes assuming a constant natural mortality rate and known annual catches. We use a simple catch equation that can be solved explicitly each year for the exploitation rate. Previous work suggests that sea surface temperature (SST) has significant predictive power for both year class strength and annual growth for snapper. We include SST predictors over appropriate months for both processes. We allow both length- and age-length dependent growth and use parametric growth functions for both mean growth and variability around the mean. We do not model maturation, cannibalism or prey mortality, as we have little or no data relating to these processes for snapper. Our age-length matrix includes fish from age 0 y, although lack of data for the early years of life means that our modelled natural mortality and growth are somewhat nominal. Fish accumulate in a maximum age column of the matrix but not in a manner that assumes constancy of mean length. The model does not distinguish the sexes.

Our growth model, which takes into account both between-year and between-fish variability, is described by Gilbert et al. (this issue a). Between-year variability has often been reported (Brander 2000, Ottersen and Loeng 2000, Cardinale and Modin 1999, Clark et al. 1999, Shelton et al. 1999, Campana 1996, Campana et al. 1995, Mehl and Sunnanå 1991). Millar et al. (1999) showed that SST was a good predictor of annual growth for Hauraki Gulf/Bay of Plenty snapper. The influence of temperature on recruitment of snapper has been observed (Gilbert and Taylor 2001, Davies and McKenzie 2001, Gilbert et al. 2000, Francis et al. 1997), as it has for many other species (Ottersen and Loeng 2000, Francis et al. 1989, Shepherd et al. 1984, MacLean et al. 1981, Sutcliffe et al. 1977). In our model mean SST over particular months is positively related to growth. There is the potential for the combined effects to amplify each other, as they both influence stock biomass and thus may need to be taken into account in stock assessment for fisheries management purposes.

Parameters were estimated using maximum likelihood based on distributional assumptions regarding the observational data. The data that we fitted the model to were: 26 commercial catch proportions at age and length estimates and 11 research trawl catch proportions at age and length estimates, four commercial proportions at age estimates, two tag-recapture estimates of numbers by length class and a catch per unit effort relative abundance index 11 years long, together with sea surface and air temperature data.

Our primary purpose was to produce a better model of the processes governing fish population dynamics so that better stock assessment could be carried out for the Hauraki Gulf/Bay of Plenty snapper stock and for other stocks for which appropriate data exist. By obtaining better estimates of current and former stock states and a better understanding of the factors governing them, we might hope to manage a fishery better. In particular, projections of the effects of future catches might be better assessed. The present paper is not however a stock assessment. It is one of a set of three papers describing: the age-length structured model (present paper), the growth component of that model (Gilbert et al. this issue a) and a comparison between estimates from this and an age-structured model (Davies et al. this issue c).

Population dynamics

The population dynamics are modelled by annually updating the age and length state matrix. The processes that achieve this take place in the following sequence: (1) all fish age by one year except those in the maximum age class; (2) the new year-class enters the 0-year-old class; (3) pre-fishing natural mortality occurs; (4) fishing mortality occurs; (5) post-fishing natural mortality occurs; (6) fish growth occurs. This sequence is somewhat arbitrary, but experience has shown that changing the sequence makes no essential difference to estimates.

Parameterisation

Our general approach has been to seek parametric functions that describe processes with a minimum number of parameters and to parameterise functions in an optimal manner. Where possible we have sought parameters that are orthogonal and that are independent of the functional form of the modelled process. For example, the growth increment equation that is equivalent to individual von Bertalanffy growth is a linear function of length, l. It can be expressed using the parameters, k and L_{∞} . Alternatively, it could be expressed using parameters equal to the size of the growth increment at l = 10 cm and at l = 30 cm, μ_{10} and μ_{30} . We estimate parameters by minimising a negative log-likelihood function. Broadly speaking, minimisation works best when parameters are orthogonal, especially in the neighbourhood of the minimum. This means that the conditional minimum of the negative log-likelihood with respect to a parameter does not depend on the conditioning values of the other parameters. In general, orthogonality depends on both the model and the data. However, it is possible to achieve approximate orthogonality for typical datasets by appropriate parameterisations. For example, the von Bertalanffy parameterisation of a linear growth increment model tends to be non-orthogonal. An increase in L_{∞} will tend to result in the conditional minimum of the negative log-likelihood occurring at a decreased value of k. The parameterisation using μ_{10} and μ_{30} is in general more nearly orthogonal in the neighbourhood of the minimum of the negative log-likelihood. It also has the advantage that without any change in the meaning of the parameters it could be used for the two-parameter exponential growth increment function that was found to fit the data best (see below).

<u>Recruitment</u>

Fish enter the age-length matrix at age 0 y and length l_0 cm. Entry of fish over a distribution of lengths around l_0 was tested, but did not improve the model fit to the data. The youngest observed fish were recorded in research trawl catches aged 1 y. We do not model the growth stages from egg to juvenile fish. Hence, the estimated l_0

is a nominal value that is somewhat analogous to estimates of the parameter t_0 in the von Bertalanffy growth function, obtained from data that does not contain lengths of 0-year-olds. The parameter l_0 does not have a biological meaning but is simply a value that generates distributions of length at older ages that fit observations.

The year class strength (YCS) parameters are multipliers of a virgin recruitment parameter R. They were constrained to have a mean of one for the modelled period, 1970–2000. We estimate 17 YCS parameters (r_{1980} ... r_{1996} : see below). For other years we use the exponential relationship between snapper YCS and SST that has been observed (Gilbert and Taylor 2001, Davies and McKenzie 2001, Gilbert et al. 2000, Francis et al. 1997). YCS for year y,

$$r_y = e^{\alpha + \beta \times^{OBS} T_y}$$

where ${}^{OBS}T_{y}$ is the observed mean SST deviation from normal for a fixed season during year y. We reparameterise this function to give,

$$r_y = \rho_0^{1-2\times^{\text{OBS}} T_y} \rho_{0.5}^{2\times^{\text{OBS}} T_y}$$

where ρ_0 is the YCS when ${}^{OBS}T_y = 0 \text{ C}^\circ$ and $\rho_{0.5}$ is the YCS when ${}^{OBS}T_y = 0.5 \text{ C}^\circ$. For periods where SST is not available and for the initialisation of the oldest age classes in the age-length matrix we set the YCS's to one (virgin recruitment).

Natural and fishing mortality

We model fishing as an instantaneous 'mid-year' event that occurs between two periods in which only natural mortality takes place,

$$c_{lak} = F_{lk} e^{-pM} n_{la}$$

where c_{lak} is the catch in numbers at length *l*, age *a*, by method *k*, F_{lk} is the fishing mortality (exploitation rate) at length *l*, by method *k*, *M* is the natural mortality, $p \le 1$ is the proportion of annual natural mortality that occurs before fishing and n_{la} is the number at length *l* and age *a* in the population matrix at the start of the year. The parameter *p* was set to 0.25 as a greater part of the catch tends to be taken at the start of the fishing year in the spring and summer, whereas most natural mortality is likely to occur in winter. However the results are not sensitive to *p*. The Baranov catch equation, which models fishing and natural mortality as concurrent, continuous, constant rate processes, is commonly used. The instantaneous, mid-year catch equation is more convenient to use because fishing mortality can be calculated explicitly from the annual catch, which is not possible with the Baranov equation. It is a first order approximation to the Baranov equation but neither is essentially more realistic than the other.

We obtain the fishing mortality at length and method from a selectivity curve, S_{lk} , that is constant over time, and an overall fishing mortality by method, $F_{.k}$,

$$F_{lk} = S_{lk}F_{k}$$

Selectivity at length l, for fishing method k, is defined by,

$$S_{lk} = \begin{cases} 0.5 \left(\frac{l - L_{Mk}}{L_{Lk} - L_{Mk}} \right)^2 & l \le L_{Mk} \\ 0.5 \left(\frac{l - L_{Mk}}{L_{Rk} - L_{Mk}} \right)^2 & l > L_{Mk} \end{cases}$$

where $L_{Lk} < L_{Mk}$ and $L_{Rk} > L_{Mk}$. This function is made up of the left- and right-hand limbs of two normal probability density functions that join at a maximum at $l = L_{Mk}$. The maximum selectivity, $S_{L_{Mk}k} = 1$. The parameters L_{Lk} and L_{Rk} are the lengths at which selectivity falls to 0.5 in the left and right limbs. The subscript k takes values: 1 =longline (all set line types), 2 =single trawl, 3 =Danish seine and 4 =other (small catches primarily by pair trawl, set net and beach seine); 5 = recreational fishing (primarily hand line); and 8 = research trawl (using finer codend mesh than commercial trawl and including fishing in areas closed to commercial trawling). Catch weight by method k,

$$C_{k} = \sum_{l=l_{\text{MLS}}}^{l_{\text{Max}}} \left(w_{l} \sum_{a=0}^{a_{\text{Max}}} c_{lak} \right)$$

where l_{MLS} and l_{Max} are the minimum legal size and maximum lengths, respectively, a_{Max} is the maximum age and w_l is the mean weight of fish of length l. The variables a_{Max} and l_{Max} were set to 30 y and 70 cm respectively. The data showed fish longer than 70 cm to be extremely rare. Hence we can obtain an explicit expression for F_k by,

$$C_{k} = F_{\cdot k} e^{-pM} \sum_{l=l_{\text{MLS}}}^{l_{\text{Max}}} \left(S_{lk} w_{l} \sum_{a=0}^{a_{\text{Max}}} n_{la} \right)$$
$$\therefore F_{\cdot k} = \frac{C_{k}}{e^{-pM} \sum_{l=l_{\text{MLS}}}^{l_{\text{Max}}} \left(S_{lk} w_{l} \sum_{a=0}^{a_{\text{Max}}} n_{la} \right)}$$

The natural mortality that occurs after fishing, reduces the remaining numbers by the factor $e^{-(1-p)M}$. Hence, the number of fish remaining at length l and age a after mortality but before growth is given by,

$$n_{la}' = \begin{cases} \left(1 - \zeta_k \sum_k F_{lk}\right) e^{-M} n_{la} & \text{where } l \le l_{\text{MLS}} \\ \left(1 - \sum_k F_{lk}\right) e^{-M} n_{la} & \text{where } l > l_{\text{MLS}} \end{cases}$$

where ζ_k is the proportion of pre-recruits returned to the sea by method k that die.

<u>Growth</u>

We model between-year and between-fish growth variation by calculating each year the distribution of growth increments that will be experienced by fish of a particular age and length. A full description of the growth model is given by Gilbert et al. (this issue a). The growth increment varies around a mean that is primarily a function of length. Between-year variation in the mean is modelled by an annual multiplicative factor that applies to all length classes. As well as length-dependent growth our model allows a growth factor that depends on both age and length. Fish that have got ahead of their year-class will tend to grow faster than their equal sized, older peers, and conversely. Hence, each vector of numbers at age requires a unique matrix multiplier to generate the next year's numbers at age vector. The full expression for the mean growth increment for a fish of length l and age a in year y is,

$$\mu_{lay}' = \left\{ 1 + \frac{2}{\pi} \left(\phi_{\infty} - 1 \right) \tan^{-1} \left[2 \tan \left[\frac{\pi}{2} \left(\frac{\phi_{1,5} - 1}{\phi_{\infty} - 1} \right) \right] \times \left\{ \frac{l}{\overline{l_a}} - 1 \right\} \right] \right\} \times \left\{ 1 + 2(\gamma_{0,5} - 1)^{\text{OBS}} T_y \right\} \times \left\{ \left(\frac{\mu_{30}}{\mu_{10}} \right)^{l/20} \frac{\mu_{10}^{3/2}}{\mu_{30}^{3/2}} \right\}$$

where μ_{10} and μ_{30} are the expected growth increments at lengths 10 and 30 cm, $\mu_{10} > 0$ and $\mu_{10} > \mu_{30}$, $\gamma_{0.5}$ is the growth factor when ${}^{OBS}T_y = 0.5^{\circ}$ C, \bar{l}_a is the mean length at age a, $\phi_{1.5}$ is the factor that applies when $l = 1.5\bar{l}_a$, ϕ_{∞} is the asymptotic agelength factor and $0 \le \phi_{\infty} \le 2$. The factor in the second braces may alternatively be replaced by an annual growth factor parameter g_y . Alternative functional forms for each set of braces were found to fit less well.

The growth increment Δl for fish of length l and age a in year y was assumed to be distributed according to a lognormal density function,

$$f(\Delta I) = \frac{1}{\sqrt{2\pi}\sigma_l \Delta I} \exp\left[-\frac{1}{2} \left(\frac{\log(\Delta I) - \log(\mu_{loy}') + \frac{1}{2}\sigma_l^2}{\sigma_l}\right)^2\right]$$

The standard deviation parameter,

 $\sigma_{l} = \begin{cases} \varsigma_{1} \left(\mu_{lay}^{\prime} \right)^{\psi} & \text{where } l < l^{*} \\ \varsigma_{2} \left(\mu_{lay}^{\prime} \right)^{\psi} & \text{where } l \ge l^{*} \end{cases}$

where $\varsigma_1, \varsigma_2, \psi$ and l^* are estimated parameters. In the case where $\varsigma_1 = \varsigma_2$ and $\psi = 0$, σ_l is the coefficient of variation (c.v.) of Δl (approximately) and is independent of μ'_{kay} and l. However we found that a dependence on both l and μ'_{kay} was necessary to account for the pattern of variability in Δl . The normal distribution with the negative tail lumped at zero was tested as a possible alternative model for between-fish growth variability, but performed less well. There were positive skews observed in the distributions of lengths at age from about age 4 y onwards and the positive skews in the lognormal increments satisfactorily generate these.

The continuous density function for Δl is integrated in segments to give the transition proportions. We adopt the convention that fish in length class l are all of length $l + \frac{1}{2}$ cm. The integral from 0 to $\frac{1}{2}$ cm gives the proportion that remain in the same length cell, that from $\frac{1}{2}$ to $\frac{1}{2}$ cm gives the proportion that grow to the next length cell, etc. Hence, the number of fish of length l', age a+1, at the start of the next year,

$$n_{l'a+1} = \sum_{l=l_0}^{l'} \left\{ n_{la}' \int_{\max(0,l'-l-\frac{1}{2})}^{l'-l+\frac{1}{2}} f(\Delta l) d(\Delta l) \right\}$$

where n'_{la} denotes numbers after recruitment and mortality. Fish in the maximum length cell remained there. In order to avoid small proportions of fish making unrealistically large growth increments, integrals less than 0.005 were set to zero and the remaining proportions rescaled to sum to one. This truncation caused the effective mean increment for age *a* and year *y* to be considerably smaller than μ'_{lay} when length $l > l^*$ (see Gilbert et al. this issue a).

Initialisation

The population state matrix at the start of the modelled period is specified by two estimated total annual fishing mortality parameters, F_1 and F_2 . Firstly, we generate an equilibrium matrix for 1941 assuming constant virgin recruitment, constant mean growth and constant fishing mortality equal to F_2 . Then we run the model from 1942 to 1949 under constant fishing mortality equal to F_2 but with the YCS parameters and the annual growth factors determined by the SST-based functions. Finally we run the model from 1950 to 1969 under constant fishing mortality equal to F_1 and with YCS and growth again determined by SST. No catch data are used to generate the 1970 state matrix and the negative log-likelihood does not include observations prior to 1970. The mortalities F_1 and F_2 are applied assuming a flat selectivity curve to all length classes above MLS. Constraints $F_1 > 0.075$ y⁻¹ and $F_2 < F_1$ were applied to ensure broad consistency with fishery history. For most model fits, estimates were at or near these constraints.

Data

The model was fitted to estimated proportions of fish caught at age and length by commercial longline, single trawl and Danish seine and by research trawl (Table 1). Other data included the estimated proportions caught at age by Danish seine, a longline catch per unit effort (CPUE) index of abundance, and population numbers at length estimated from tag-recapture experiments. Gilbert et al. (2000) provided a description of these data.

Because the variability amongst distributions of age and length in catches of fish is greater than would be predicted by simple random sampling, the precision of an estimate of proportions at age and length is less than might be inferred from the sample size. We treat the proportions estimates as though they come from simple random samples of the catch, but apply an effective sample size, v, that is less than the actual sample size, to account for the spatial heterogeneity. In most years our estimates were based on an age-length key obtained from fish from both commercial and research samples. For each method, catch proportions at length were estimated and then applied to the age-length key to obtain the estimated proportions at age and length. Because the same age-length key was applied, the estimates for different methods in the same year are not independent. We therefore reduce their effective sample size to reduce their weighting. In a few cases separate direct age samples were taken for each method. For a particular year's samples, v was determined by an arbitrary formula,

$$v = \frac{\left(\frac{\sqrt{K \times Z}}{5}\right)}{\sqrt{N}} \text{ where } Z = 5L + S$$

where L was the number of sampled commercial landings contributing to the agelength key, S was the number of research trawl stations contributing to the age-length key, K was the number of otoliths that made up the age-length key, and N was the number of fishing method length samples to which the same age-length key was applied. This formulation assumed that the random nature of research trawl surveys meant that five research stations were equivalent to a commercial landing. When N > 1 we have several closely related age-length proportion estimates that are each assigned reduced sample sizes and hence higher standard errors. The values obtained for v are presented in Table 1.

A SST measurement is taken daily at 9:00 a.m. at the Leigh Marine Laboratory climate station located in the outer Hauraki Gulf. This time series starts in 1967 and was combined with air temperature data from 1911 by Gilbert et al. (2000) to produce a nominal monthly mean SST time series from 1911 to 2001.

Fitting

For each data type we specify a probability distribution for the observational error. Hence we obtain a total negative log-likelihood that is minimised to effect the estimation of parameters. Constant terms in the log-likelihood are ignored. In general the distributional assumptions are only approximations of complex random processes and hence ad hoc modifications to the likelihood are required in some instances.

Proportions at age and length

Model estimates of the numbers caught at age and length by method are fitted to the observed proportions. Let ${}^{OBS}p_{lak}$ be an observed proportion in some year. Then the proportion estimated from the model,

$$p_{lak} = \frac{c_{lak}}{\sum_{l,a} c_{lak}}$$

The negative log-likelihood term for a year's data, based on the multinomial distribution,

$$\Lambda_{\rm AL} = -\sum_{l,a,k} v_k \times {}^{\rm OBS} p_{lak} \times \log p_{lak}$$

where v_k is the effective sample size (see above). The quantity $v_k \times {}^{OBS} p_{lak}$ was not necessarily an integer. Therefore Λ_{AL} is not strictly a multinomial negative log-likelihood. For observations (rare) where ${}^{OBS} p_{lak} > 0$, but $p_{lak} = 0$, we arbitrarily set p_{lak} to 10^{-7} . Likelihood based on lognormal and robust normal distributions were also tried, but led to less satisfactory residuals. In the case of the lognormal distribution this was largely due to a high frequency of observations of zero proportions that had to be replaced by a highly influential but arbitrary non-zero value.

Proportions at age

Model estimates of the numbers caught at age by method were fitted to the observed proportions. Let ${}^{OBS}p_{ak}$ be an observed proportion in some year. Then the proportion estimated from the model,

$$p_{ak} = \sum_{l} p_{lak}$$

The negative log-likelihood term for a year's data, based on the lognormal distribution,

$$\Lambda_{A} = \sum_{a,k} \left[\log(\sigma_{ak}) + \frac{1}{2\sigma_{ak}^{2}} \left(\log\left({}^{\text{OBS}}p_{ak} \right) - \log\left(p_{ak} \right) + \frac{\sigma_{ak}^{2}}{2} \right)^{2} \right]$$

where σ_{ak} was obtained assuming that the variance for each age proportion was the same as would occur under binomially distributed deviates, $\sigma_{ak} = \sqrt{\log\left(1 + \frac{(1 - p_{ak})}{v_k p_{ak}}\right)}$,

where v_k is the effective sample size (see above). A zero observation cannot occur in a lognormal deviate, but is a possible observed proportion at age. Therefore Λ_A is not strictly a lognormal negative log-likelihood. For observations where $p_{ak} = 0$ (rare) we arbitrarily set p_{ak} to 10^{-7} . Where $^{OBS}p_{ak} = 0$ (also rare) the corresponding term in the expression for Λ_A was set to zero.

Tag-recapture numbers at length

Model estimates of the numbers at length in the population are fitted to the tagrecapture estimates. This is similar to the fitting of proportions at age, except that here we deal with absolute numbers in the population rather than proportions in the catch,

$$n_l = \sum_{\alpha} n_{l\alpha}$$

The negative log-likelihood term for each estimate, based on the lognormal distribution,

$$\Lambda_{\rm L} = \sum_{l} \left[\log(\sigma_l) + \frac{1}{2\sigma_l^2} \left(\log\left({}^{\rm OBS}n_l \right) - \log\left(n_l\right) + \frac{\sigma_l^2}{2} \right)^2 \right]$$

where ${}^{OBS}n_l$ and n_l are the estimate and the model fitted numbers at length, *l*. Here the index *l* is used to denote groups of cm length classes (see Table 1). The standard deviation σ_l was set to 0.25 for all length classes based on the probable precision of the estimates. As before, Λ_A is not strictly a lognormal negative log-likelihood.

<u>Relative stock biomass index</u>

The "vulnerable stock biomass" for a method k' = longline, in some year, is obtained by calculating the biomass of the population after 40% of the year's catch has been taken (corresponding to the centre of the longline season). The longline selectivity curve is also applied to give vulnerable stock biomass,

$$V_{k'} = \mathrm{e}^{-pM} \sum_{l=l_{\mathrm{MLS}}}^{l_{\mathrm{Max}}} \left[\left(1 - 0.4 \sum_{k} S_{lk} F_{.k} \right) S_{lk'} w_l \sum_{a} n_{la} \right]$$

If we have a longline catch per unit effort relative biomass index for that year, $I_{k'}$, its expected value is related to $V_{k'}$ by a catchability coefficient, $q_{k'}$, $E(I_{k'}) = q_{k'}V_{k'}$.

The negative log-likelihood term for the observed index $OBS_{I_{k'}}$, based on the lognormal distribution,

$$\Lambda_{\text{CPUE}} = \log(\sigma_{\text{CPUE}}) + \frac{1}{2\sigma_{\text{CPUE}}^2} \left(\log\left(^{\text{OBS}}I_{k'}\right) - \log(q_{k'}V_{k'}) + \frac{\sigma_{\text{CPUE}}^2}{2}\right)^2$$

where σ_{CPUE} was set to 0.2, which is consistent with the recommendation of Francis et al. (2001). The catchability, $q_{k'}$, may be estimated directly using the differential calculus by

$$q_{k'} = \exp\left[\frac{1}{n}\sum_{y} \left(\log\left(OBSI_{k'y}\right) - \log(V_{k'})\right) + \frac{\sigma_{CPUE}^2}{2}\right]$$

where n is the number of observations and the extra subscript y denotes year.

Temperature recruitment relationship

We take the SST data to be quantities related to YCS's that are observed with random error (e.g., they come from a single location rather than from the whole population area). Hence we derive a likelihood for them. Where the YCS, r_y is an estimated parameter (1980–96), we can rearrange the equation given above to give an expression for the expected value of the SST,

$$\mathrm{E}(T_{y}) = \frac{\log r_{y} - \log \rho_{0}}{2(\log \rho_{0.5} - \log \rho_{0})}$$

The negative log-likelihood term for the observed value ${}^{OBS}T_{y}$, based on the normal distribution,

$$\Lambda_{\rm YCS} = \frac{1}{2\sigma_{\rm YCS}^2} \left(\frac{{\rm OBS}T_y - \log \rho_0}{2\left(\log \rho_{0.5} - \log \rho_0\right)} \right)^2$$

where $\sigma_{\rm YCS}$ was set to 0.5.

Temperature growth relationship

Again the SST's are assumed to be observed with error. Where the growth factor g_y is an estimated parameter (1991–2000), we can rearrange the equation given above to give an expression for the expected value of the SST. Because the SST variable relevant here refers to a different season than that for the YCS relationship we distinguish it by a dash,

$$E(T'_{y}) = \frac{g_{y}-1}{2(\gamma_{0.5}-1)}$$

The negative log-likelihood term for the observed value ${}^{OBS}T'_{y}$, based on the normal distribution,

$$\Lambda_{\rm G} = \frac{1}{2\sigma_{\rm G}^2} \left({}^{\rm OBS}T'_y - \frac{g_y - 1}{2(\gamma_{0.5} - 1)} \right)^2$$

where $\sigma_{\rm G}$ was set to 1.0.

We used a Simplex minimiser (Amoeba) that allowed a maximum of 50 parameters to be estimated. For this reason we were not able to estimate the YCS parameters and the growth factors for all years within the modelled period. We therefore estimated individual YCS's for 1980–96 and growth factors for 1991–2000. These periods were those for which our data was most informative and those that would have the most influence on current stock state.

Diagnostics

Diagnostics of the fit to the observed proportions at age and length were based on standardised residuals,

$$\varepsilon_{lak} = \frac{\frac{OBS}{p_{lak} - p_{lak}}}{\frac{S_{lak}}{S_{lak}}}$$

where s_{lak} is the standard deviation for the multinomial distribution (ignoring covariances which are very small here),

$$s_{lak} = \sqrt{\frac{p_{lak}(1 - p_{lak})}{\nu_k}}$$

Results

To elucidate the model structures that were successful in explaining the data we will start with a simple model and describe the effects of successively adding features. Modellers will understand from experience that the tidy sequence of structures that we describe does not necessarily correspond to the temporal sequence that we followed in developing the model. The models described are listed in Table 2, where the successive reductions in the Akaike Information Criterion (AIC) are presented.

The simplest model, SIMPL, had constant year class strengths and constant mean growth. Within-year growth variability was lognormal and was described by a single parameter, ς_1 , the standard deviation of the log of the mean growth increment (approximately constant c.v.). The parameter ψ was set to zero and ς_2 made equal to ς_1 . This model failed most noticeably by predicting an excessive spread of length at age for fish younger than 9 y (Fig. 1). Its failings were only apparent in the research trawl age-length data, because the commercial minimum legal size is 25 cm. The distributions of length at age shown in the research trawl data were fitted better by the model, CONST, where $\varsigma_1, \varsigma_2, \psi$ and l^* were all estimated (Fig. 1).

Our age data show considerable YCS variability. We added YCS variability to the model structure in two steps. In the first model, RSST, a single parameter, $\rho_{0.5}$, predicted YCS from SST. In the second, GCONST, individual YCS's were estimated for 1980–96. The age marginals for the age-length data do not fit well when YCS is constant (Fig. 2). RSST and GCONST gave substantial successive reductions to the AIC indicating improvements to the fit.

We added growth variability in three steps. In the first, GSST, the parameter $\gamma_{0.5}$ predicted the annual growth factor from SST. In the second, DEL0, individual growth factors were estimated for 1991–2000, and in the third, MLE, an age-length effect was added to the growth function requiring two further parameters $\phi_{1.5}$ and ϕ_{∞} . Each step improved the AIC (Table 2), but the improvement to fits to the length marginals for the age-length data are often not visually apparent (Fig. 3). The improved fit to the irregular pattern of mean lengths at age is apparent in the MLE estimates (Fig. 1). The improvement in fit from DEL0 to MLE is modest but can be seen by comparing the overall mean age-length residuals (Fig. 4). The MLE model better accommodates the small proportion of "stunted" or "giant" fish, although there remain some outliers.

Alternative models for mean growth increment such as linear or power functions, alternative models for the relationship between SST and mean growth, for growth variability, and for the increase in growth variability with length, were tested during the development of the model structure but those described above are the best we could find on the basis of the AIC.

MLE fit to proportions at age and length

The mean standardised residual at age and length for all methods and all years, reveals a relatively good fit of the MLE model as indicated by mean residuals close to zero through the main body of the distribution (Fig. 4). Five large positive residuals are visible on the periphery of the distribution for extremely slow-growing, old fish. These observations were rare (on average less than 0.5% of the observed distribution). It is unlikely that these observed extremes in length at age are completely attributable to measurement error, as observations of stunted and giant snapper have been reported previously (Paul 1976). Our failure to find a model that completely explains them is perhaps more a blow to our pride than a major shortcoming of our model.

A plot of the mean, 5 and 95 percentiles of the proportions at age and length standardised residuals against length, for each gear type over all years (Fig. 5) illustrates the general goodness of fit of the model. The means are generally close to zero. The model appears to have a very small amount of negative bias for large, longline-caught fish and for mid-length single trawl and Danish seine fish. A small oscillation in the research trawl residuals between 11 and 15 cm is discussed below. The percentiles suggest some positive skewness at the larger lengths, which is expected. The residuals are also generally smaller than expected under the multinomial assumption and tend to decrease with decreasing expected proportion. Interpretation of the residuals is complicated by the fact that the effective sample sizes were reduced where multiple methods employed the same age-length key (see above). Nevertheless the residuals suggest that the effective sample sizes were somewhat too low and also that the data are not wholly consistent with the multinomial assumption.

Difficulties were found in achieving good fits to research trawl length marginals that are comprised largely of fish less than 25 cm. These distributions are variable between years with length modes varying due to growth and year class strength fluctuations. In some years the observed annual growth variation appeared to differ between methods, e.g., in 1994 the research trawl modes are at systematically larger lengths than those predicted by MLE whereas the longline mode is at a smaller length (Fig. 3). For some years, none of the growth models performed well for some methods, e.g., longline in 1985, but achieved reasonably good fits to other methods, e.g., research trawl in 1985. An oscillation in the research trawl residuals between 11 and 15 cm is evident in Fig. 5. This appears to be due to lack of fit in the mean and spread of lengths at ages 1 and 2 y in some research samples, rather than a failing of the selectivity function. The observed 1-, 2- and 3-year-old modes were generally narrower than the predicted modes (Fig. 3). The wider modes appear to be best average predictions that compensate for the failure of the model to consistently predict the highly variable centres of the observed modes.

MLE fit to proportions at age

The effective sample sizes for the proportions at age were small (Table 1) and therefore these data are not influential. They perhaps have some limited influence on the modelled proportion of 20+y fish in the population at the start of the modelled period. The residuals showed moderately high variances but were on average close to zero (results not shown).

MLE fit to tag-recapture estimates of numbers at length

The model fit to the numbers at length estimated from the tag-recapture experiment in 1994 was improved for the smaller length classes by estimating the annual growth factors individually (Fig. 6). For 1985, the number in the 25–28 cm class was considerably over-estimated in all models, as were the 34–36, 37–40 and 41–50 cm classes for 1994. We did not estimate individual growth factors during the 1980's due to the inability of our minimiser to estimate more than 50 parameters. If we had this may have improved the fit to the 25–28 cm class in 1985. The residuals showed somewhat greater variability than would be expected from their assumed standard deviations.

MLE fit to CPUE abundance indices

The MLE, GCONST, and GSST models all provide fits to the broadly flat longline CPUE abundance index consistent with the assumed c.v. = 0.20 (Fig. 7).

Sea surface temperature relationships

Significantly better fits were obtained for models that related variability in YCS and mean annual growth to SST (RSST and GSST), than those that had constant YCS and growth (Table 2). We determined by trial and error that amongst 6-monthly periods, December to May when a year-class was spawned was the best predictor of YCS. April to September was the best predictor of annual growth. Because of serial correlation in monthly temperatures there were several 6-monthly periods overlapping those given, that gave predictors that were almost as good. Both the recruitment and growth relationships were positive.

Trends in abundance

Consistently low temperatures during the 1991 to 1994 *El Niño* produced sustained low growth. The biomass of fish larger than MLS that was estimated by the MLE model reflects this effect, with a 20% decline from 1991 to 1995 when total catch did not change greatly (Fig. 8). Assuming constant growth (GCONST) results in a flat biomass trajectory over the period. The individually estimated growth factors for the 1990's are systematically lower than those predicted by SST (Gilbert et al. this issue a). This results in the MLE model having a lower trajectory than that for GSST.

Selectivity at length curves

Estimation of the selectivity curves for the "other" commercial and the noncommercial methods was not possible, since no samples were available to fit to. The model includes possible discarded catch below the MLS via the left-hand limbs of selectivity curves. Discard mortalities are modelled (see above). However, estimating selectivity curves that have their maxima not far above the MLS was not satisfactory, as most fish less than this size are not landed and were therefore not present in the samples. We found it necessary to fix L_L and L_M for single trawl and the L_M for Danish seine. We also found it useful to fix L_R to a large length for longline. When it

. این بعد اما توجیدین الماهد الیه وم تنویه المانی (الحاد was estimated it invariably took a large value. There are large differences between the selectivity at length curves for the research trawl, single trawl, and longline methods, with Danish seine and longline estimates being similar (Fig. 9). Research trawl is strongly selective for smaller fish with maximum selectivity occurring at 16 cm, and low selectivity for lengths above 40 cm.

Management controls

We briefly describe an example of the use of the model to evaluate the effects of length-based management options. The MLE model was run forward with deterministic virgin recruitment for 20 years from 2001, but with changes to the MLS for specified methods. An increase in the MLS from 25 to 30 cm was applied to the longline method and this resulted in a very slight increase in deterministic maximum sustainable yield (MSY, Table 3). A similar increase from 27 to 30 cm for the recreational method resulted in a very slight decline in MSY. In both cases changes in other relevant variables were also very slight. We conclude that the benefits of MLS increases in reducing mortality on smaller fish is offset by the discard mortality, assumed to be 20% for both methods. The very slight differences between the options are caused by the selectivity differences between the methods.

Discussion

By defining the stock state by a matrix of numbers at age and length and using functions that describe between-year and within-year variability in mean growth and variability in year class strength, our model is able to predict population age and length compositions through time. The distributions of length at age are not only affected by the between-year growth variations but they are also dynamically modified by the removal of catch according to the selectivity curves of the fishing methods. The model performs better in predicting length at age, and hence mean weight at age, than is possible by age-structured models. Hence our estimates of trends in population biomass are better (see Davies et al. this issue c). Guldbrandsen Frøysa et al. (2002) developed a similårly age and length structured model named Fleksibest to capture the effects on population biomass of the substantial variability in growth in sub-arctic stocks. Our modelling showed that the more moderate variations in growth between years in a temperate species were sufficient to have moderate effects on population biomass.

Guldbrandsen Frøysa et al. (2002) suggested expressing growth increment as a power function of the reciprocal of length. Millar et al. (1999) found that this function (including an annual SST term) fitted Hauraki Gulf snapper data better than a linear (von Bertalanffy) function of length. They fitted their model to mean lengths at age (from age 2 y) from the research trawl data that we have used (excluding 1998 and 2001). Our estimate of the selectivity curve for research trawl has maximum catchability at 16 cm and sharply declining catchability above this. Hence, the sample mean lengths of older year-classes were biased downwards. We used both research trawl and commercial age-length samples and included the effects of estimated selectivity curves. We found that growth increments could be best modelled with an exponential function. We found that Millar et al.'s formulation, and modifications of it, did not fit as well, even when we added a length offset parameter. Their suggestion that the power function cannot satisfactorily fit both growth between 0 and 2 y and growth of the oldest fish appears to be correct. Similarly, the "hockey stick" function

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described by Cranfield et al. (1996), which is linear but has an appended asymptotic curve at the right hand end, did not fit the data as well as the exponential function.

Several parametric functions were required to explain the observed age-length data. We started with a simple exponential function of length for mean growth increment. We found that this had to be modified by an annual factor. Further, the resulting function had to be modified by an age-length effect whereby the growth of fish that have got ahead of the mean length of their year-class is greater than that of their equal-sized, older peers and conversely. Individual variability around mean growth was found to increase substantially at about the length at which 50% are mature and a four-parameter function was required to describe within-year variability (see Gilbert et al. this issue a). All these functions were estimated concurrently with selectivity curves and so that they are proper estimates of population parameters rather than estimates of characteristics of the landed catch, as is the case for the estimates of Millar et al. (1999).

Annual SST was a good proxy for predicting variability in mean growth, but individually estimated annual growth factors deviated somewhat from the SST-growth relationship. It is possible that the location of measurement of the SST was not representative of the conditions affecting the entire population (see Brander 1995). It is more likely that SST does not fully determine the conditions that contribute to growth variability and that the use of a single predictor may sometimes produce poor predictions (see Sinclair et al. 2002).

Because the influence of good or bad growing conditions is greatest when fish are growing fastest, the SST-related effects on the growth in juvenile fish persist for several years, even when conditions reverse. Brander (2000) found that for cod, SST effects on growth in the first year of life accounted for variability in weight at age of cod for up to 6 years. Our model predicted a similar inertial effect on population biomass in the years following sustained poor or good growth. We found that the early 1970's and the early 1990's were respectively good and poor growth periods whose effects persisted.

Examination of the residuals from the fit to the proportions at age and length with respect to method, year, age, length, year class and predicted proportion showed no serious lack of fit and few unsatisfactory patterns. A pattern in the research trawl residuals for 11–15 cm fish suggests that a more complex structure for the mean and variance of the growth increments of 1- and 2-year-olds should be investigated. Between-year variability in observed age-length samples may be attributed to measurement error (Millar et al. 1999), spatial heterogeneity in growth rates causing some research samples to be unrepresentative (Paul 1976), variable length in spawning and larval periods causing mean length at age of 1-year-olds to vary between years (Francis 1994a), or differences in the processes impacting on sub-adult and adult snapper growth (Francis 1994b). Use of a single factor for annual growth variation of all length classes is parsimonious and was broadly consistent with the data, but a more complex model may be necessary.

Generally, the MLE model fits to the four different data types and the SST recruitment and growth relationships were satisfactory. The variability of the residuals for the tag-recapture data and for the proportions at age data was somewhat higher than implied by our assumptions. There appears to be some inconsistency between the tag-recapture abundance estimates and the other data, the latter implying somewhat higher abundances. Good model fits to the proportions at age data were not possible because these data showed substantial inconsistency between YCS's in successive years.

The MLE model fit could perhaps be improved according to the AIC, by increasing the total number of parameters estimated. Estimation of individual growth factors for the whole modelled period may improve estimated length at age for the earlier years. Estimation of separate, annual, juvenile and adult growth factors may be required to account for the possibility that conditions benefiting these groups differ. Estimation of individual YCS's for the whole modelled period may improve the relative abundances of the early year-classes. An increase in the number of parameters estimated would require employing an alternative minimiser.

Davies et al. (this issue, b) quantify the differences between a conventional agestructured model that assumes constant growth and the model presented here, and show that estimates of biomass by the simpler model can be biased. As a stock assessment tool to determine current stock status, the present model is therefore an improvement on simple age-structured models that assume constant mean growth. Our model also has the potential to improve the accuracy of simulations that investigate the relative performance of proposed length-based management controls because of its explicit description of length-based processes in a manner that allows effects to persist in the population state matrix. Changes in MLS may be assessed for given discard mortality rates in terms of projections and equilibrium yields.

We have provided what we think is a useful model of the major features of the dynamics of the Hauraki Gulf/Bay of Plenty snapper population, that fits a substantial dataset covering 32 years of exploitation. The model is of inherent interest for the processes it describes, it could be a useful stock assessment tool and it could be used to investigate the effects of length-based management controls.

Acknowledgments

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Table 1. Summary of input data: effective sample sizes, v, (see text), methods and years for proportions caught at age and length (Age-length), and for proportions caught at age (Age); method and years of catch-per-unit-effort abundance index (CPUE); number of length classes and years of tag-recapture estimates (Tag); (- indicates no data).

Year				Age	CPUE	Tag	
	- <u></u> -	Single	Danish	Research	Danish		
	Longline	trawl	seine	trawl	seine	Longline	
1970	_	_	_	_	6.3	-	
1971	_	_	-	-	6.6	-	-
1972	-	_		-	7.1	-	_
1973	-	_	_		6.2	-	_
1975		20.6	39.9	-			_
1976	_	12.4	13.8		_	-	_
1985	88.1	88.1	88.1	88.1	_		7
1986		-	-	51.2	-	_	_
1 98 7	-	-	_	45.1		_	-
1988	-	-	_	13.6	-	<u> </u>	-
1990	20.0	20.0	-	20.0	-	1	-
1991	22.3	22.3	-	22.3	_	1	-
1 992	55.0	-	55.0	_	-	1	-
1993	32.6	-		32.6	-	1	_
1 994	24.9	24.9	24.9	24.9	-	1	8
1995	25.0	-	25.0	25.0	_	1	_
1996	51.9	-	51.9			1	. —
1997	86.6	· _	-	_	-	1	_
1998	88.0	-	_	88.0		1	
1 999	91.6	-		-	_	1	_
2000	98.3	-	_		_	1	-
2001	80.0	-	-	80.0	. –	-	-

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Table 2. Model names and corresponding component structures for recruitment and growth processes: GSTEP, individual growth variability has a stepwise change; YCST, year class strength is a function of sea surface temperature; RYCS, annual year class strengths are free parameters; GRST, annual mean growth factors are a function of sea surface temperature; GFAC, annual mean growth factors are free parameters; GAGE, annual mean growth factors are a function of age and length. The number of model parameters estimated (n), the total negative log-likelihood (A), and the Akaike Information Criterion (AIC) are given. The symbol, *, indicates that the component structures was included.

Model [†]	Component structure and corresponding parameters								
	GSTEP	YCST‡	RYCS	GRST	GFAC	GAGE	n	Λ	AIC
	ς_2, ψ, l^*	ρ _{0.5}	r ₈₀ r ₉₆	Y0.5	G 91G2000	$\phi_{1.5}, \phi_{-}$			
SIMPL	_		-	-	_	-	16	9062.7	18157.4
CONST	*	-	_	-	_	_	19	8819.4	17674.8
RSST	• 🔺	*	_		_	_	20	8739.9	17517.8
GCONS	*								17337.4
Т		*	*		_	_	37	8632.7	
GSST	*	*	*	*	_		38	8600.9	17275.8
DEL0	*	*	*	*	*	_	48	8533.2	17160.4
MLE	*	*	*	*	*	*	50	8516.8	17131.6

† Parameters common to all models: R, F_1 , F_2 , μ_{10} , μ_{30} , l_0 , ς_1 , L_{M1} , L_{R1} , L_{R2} , L_{L3} , L_{R3} , L_{M8} , L_{L8} , L_{R8} , and q. ‡ The parameter ρ_0 is determined by the requirement that mean YCS equal one for 1970–2000 and is therefore not independently estimated.

Table 3. Expected biomass in 2021, $E(B_{21})$, expected biomass in 2006 relative to B_{MSY} , $E(B_{06}/B_{MSY})$, biomass that supports maximum sustainable yield, B_{MSY} , and maximum sustainable yield, MSY. Estimates are from the MLE model, from a model where commercial longline MLS LL30, and one where recreational fishing MLS was increased to 30 cm, REC30. All biomasses are in thousands of tonnes.

	MLE	LL30	REC30
$E(B_{21})$	90.958	91.562	91.297
$E(B_{06}/B_{MSY})$	0.747	0.748	0.750
B _{MSY}	60.944	61.277	60.334
MSY	7.340	7.367	7.318



Fig. 1. Observed and predicted proportions at age and length for research trawl for 2001 and 1998. For each age-class the horizontal bar shows the observed mean length and the vertical bar the 5 and 95 percentiles. The lengths predicted by the MLE model (see Table 2) are shown in each plot by the mean (heavy solid line) and the 5 and 95 percentiles (light solid lines). In the upper plot the corresponding predictions by the SIMPL model (constant YCS, mean growth and CV around mean growth) are shown by dashed lines. In the lower plot the corresponding predictions by the CONST model (constant YCS and mean growth, but growth variance dependent on a 4-parameter function) are shown by dashed lines. A stepwise increase in variability occurs at 22 cm, which is shown by a horizontal line.



Fig. 2. Marginal proportions at age from longline and research trawl catches in selected years. Diamonds denote observed proportions. Lines denote model fits (see Table 2), CONST (solid), RSST (dash-dot-dot) and GCONST (dot).



Fig. 3. Marginal proportions at length for longline and research trawl catches in selected years. Diamonds denote observed proportions. Lines denote model fits (see Table 2) GCONST (dot), GSST (dash-dot) and MLE (solid).



Fig. 4. Mean of the standardised residuals of the proportion caught at age and length for all fishing methods over all years from fits of the MLE and DEL0 models (see Table 2).



Fig. 5. Mean, 5 and 95 percentiles of the standardised residuals, versus fish length, from the MLE model for proportions caught at age and length for the longline, single trawl, Danish seine and research trawl methods.



Fig. 6. Fits to estimates of population abundance in length classes from tag-recapture experiments carried out in 1985 and 1994. Circles denote tag-recapture estimates, lines denote models fits (see Table 2) MLE (solid), GCONST (dot), and GSST (dash-dot).



Fig. 7. Fits of model estimates of relative abundance adjusted by longline selectivity to observed longline catch per unit effort indices (dots). Lines denote model fits: MLE (solid), GCONST (dot), and GSST (dash-dot).







Fig. 9. Selectivity curves based on two normal density functions defined by the join length parameter, $L_{\rm M}$, and the left- and right-hand lengths that give 50% selectivity, $L_{\rm L}$ and $L_{\rm R}$. Not all 36 parameters were estimated. Methods are: longline (heavy solid - $L_{\rm M}$ and $L_{\rm L}$ estimated), single trawl (light solid - $L_{\rm R}$ estimated), Danish seine (dashed - $L_{\rm L}$ and $L_{\rm R}$ estimated), other commercial (thin solid - none estimated), research trawl (dash-dot - $L_{\rm M}$, $L_{\rm L}$ and $L_{\rm R}$ estimated) and non-commercial (dot - none estimated).

Section c

Davies, N.M., Gilbert, D.J. and J.R. McKenzie. In prep. The importance of growth variability in population models: an example for New Zealand snapper. *Marine and Freshwater Research*.

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Abstract

Biomass and yield estimates were derived for New Zealand snapper using a Catch-atage-LENgth-structured model (CALEN), having length-based, and temperaturedependent, growth and recruitment processes, (Gilbert et al. this issue b). These estimates were compared with those derived using a conventional Age-structured MODel (AMOD) under the assumption of constant annual growth. The AMOD estimate of constant mean weight at age differed markedly from the variable CALEN estimates that explicitly reflected the cumulative effects on cohort length frequencies of temperature-dependent growth during a cool El Niño period, length-based fishing mortality, and year class strength variability. AMOD annual biomass estimates were consistently higher than CALEN. Bias and variance in these estimates was calculated from parametric bootstraps conditioned on CALEN as a "true" population. Under the structural and error model assumptions made for the "true" population, AMOD bootstrap estimates of snapper stock biomass and status were highly positively biased. The results suggest that model uncertainty estimation conditioned upon structural model assumptions regarding growth variability is an important element in fish population studies. New Zealand sea temperatures are largely determined by El Niño Southern Oscillations, so temperature-driven growth and recruitment effects have significance for assessing and managing snapper. This may also be true for other temperate stocks exhibiting these features.

Introduction

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The importance of growth variability in fish population modelling and stock assessment is increasingly being recognised. Temperature has been cited as a possible cause of growth variability in exploitable fisheries. Species for which temperature growth effects have been described include: cod *Gadus morhua* (Taylor 1958, Brander 2000); squid *Loligo gahi* (Hatfield 2000); snapper *Pagrus auratus* (Paul 1976, Francis 1994a). Other factors thought to cause growth variability include: density-dependence (Rose et al. 2001); size-selective fishing mortality (Welch and McFarlane 1990, Sinclair et al. 2002a); timing of larval hatching (Rechlin 2000); behavioral thermoregulation (Jobling 1995); and interactions between temperature and density-dependence (Ottersen and Loeng 2000, Ottersen et al. 2002, Kristiansen et al. 2001); or interactions between temperature, density-dependence, and size-selective mortality (Smith et al. 1990). In many cases significant relationships between growth and temperature or an unspecified environmental variable (Maceina 1992) were found.

The realisation of the importance of variability in mean annual growth has prompted some fisheries modellers to modify growth functions to better account for this process. The von Bertalanffy function has been fitted to growth data with a compensating factor for temperature effects (Doerzbacher et al. 1988), or extended to include temperature effects that better account for observed annual trends in growth (Campana et al. 1995, Fontoura and Angostinho 1996). Brander (1995) was able to explain a high amount of the observed variance in mean weight-at-age for 2 to 4-yearold atlantic cod using a simple exponential model of mean weight-at-age as a function of age, and mean ambient annual temperature. Mooij and van Nes (1998) used a power function that incorporated temperature-dependence to describe somatic growth for a range of freshwater fish species. Millar et al. (1999) found that a growth model that used a power curve modified with a linear temperature function provided a better fit to a time series of research length and age data in NZ snapper than a model that did not include a temperature effect.

Given the commonality of annual growth variability in fish surprisingly few of the models routinely used for fisheries stock assessment incorporate time-variant growth mechanisms. (Pattersen et al. 2001). Variability in mean length at age may be due to temperature-growth effects, size-selective mortality, or a combination of both (Sinclair et al. 2002b). These growth variability mechanisms are often not allowed for in the calculation of mean weight at age; the failure to do so may bias some age structured population model estimates of biomass or catch. The importance of this was recognized for length-structured models (Jones 1990).

In response to evidence that temperature influences the age of maturity in atlantic cod Myers et al. (1997) fitted a temperature correlation with intrinsic rate of population increase to assess stock recovery times under average temperature regimes. Van Winkle et al. (1997) developed a feedback system model to explicitly describe the temperature dependent physiological processes of energy allocation on fish growth and reproduction. Van Winkle et al.'s approach may provide a useful basis for reviewing growth functions in conventional population models.

Although it is difficult to explicitly account for size-selective fishing mortality and variability in mean weight-at-age using age-based models, the effects have been approximated using partial recruitment functions (Gilbert et al. 2000). Prompted by an observed decadal decline in Pacific halibut mean length-at-age Clark et al. (1999) used a more explicit approach; their model estimated fishing method selectivity at length and included a time-variant growth function to describe annual cohort length compositions. An age-structured model developed by Punt et al. (2001) probably goes further than most in accounting for growth variability on the population's length composition. Their age-structured model incorporates five separate growth functions that define separate "genetic" growth paths for members of each cohort. Punt et al. apply size-selective fishing mortality to their estimated numbers at length in each growth category. Numbers at length are modified by fishing mortality, and carried through each year and thus retain the cumulative effects of size-selective fishing mortality on the cohort in accordance with the five growth path categories.

Despite the apparent utility of these extensions to age-structured population models, these models are unable to explicitly account for the cumulative effects of time-variant growth, size-selective fishing mortality, and Year Class Strength (YCS) on cohort absolute length frequencies through time. The modelling of inter-annual growth may be better achieved by explicitly estimating the numbers at length for all cohorts in the population in each year. Gilbert et al. (this issue a) developed a highly flexible parametric function that has length, age-length and annual factors for mean

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annual growth and uses log-normal distributions to describe individual growth variability. Gilbert et al. (this issue b) use this growth function in their integrated Catch-at-age-LENgth structured population model (CALEN). The basis of the CALEN model is a matrix of population age and length frequencies. This matrix is updated in every year to take into account growth, year class strength variability, and size-selective mortality. Gilbert et al.'s approach is similar to that described by Guldbrandsen Frøysa et al. (2002), but differs in a number of respects. The CALEN model takes into account both length- and age-dependent growth, and uses parametric growth functions for both mean growth and variability around the mean. CALEN also uses a simpler calculation of annual fishing mortality.

Gilbert et al. (this issue b) developed CALEN specifically to assess New Zealand snapper, a species that exhibits considerable variability in growth and YCS. There is evidence that annual variations in water temperature affect snapper growth. Francis et al. (1992a) showed water temperature could affect the rates of otolith formation and somatic growth in juvenile snapper. Although in a later paper Francis (1992b) acknowledges otoliths may not reliably record somatic growth histories. Francis (1994a) showed a significant positive correlation exists between growth rate and sea surface temperature for juvenile snapper, with winter growth being slow, and almost negligible in older fish. Earlier Paul (1976) had shown that inter-annual trends in growth of adult snapper were consistent with annual mean temperatures. A significant positive correlation was found between sea surface temperature and annual growth increments of 2-year-old fish (Davies et al. in press). However the temperature growth relationship may not be consistent over all ages; Francis (1994a) found the temperature growth response in 0+ snapper was less than that of older fish but still positively correlated. Snapper growth appears to be complex and individual growth variability is high. As a result, length distributions for the adult age classes are wide, e.g., 25 to 51 cm for fish 9 years old (Davies et al. in press). A water temperature growth relationship might explain an observed decline in mean length at age of snapper in commercial landings during the 1990s (Davies et al. in press).

In accordance to the life history classification of Rose et al. (2001), snapper is typical of the periodic life strategy, being long-lived, highly fecund, with high YCS variability. Francis (1993) showed snapper YCS indices are strongly positively correlated with mean April to June sea surface temperatures in the first year of life. The temperature growth relationship may underpin the temperature YCS relationship in that slow growth may result in higher larval or juvenile mortality. Considerable variation has been reported in the spawning period duration, and larval period duration, both of which are temperature dependent (Francis 1994b). Onset of spawning is temperature-related and may vary regionally, resulting in high variability in larval duration in the population.

These features of snapper growth and recruitment have important implications for stock assessment and management, particularly with the climatic variability caused by El Niño Southern Oscillations resulting in annual, sometimes prolonged, temperature fluctuations in the Hauraki Gulf/Bay of Plenty waters of New Zealand (Bell and Goring 1998).

We compare population estimates derived from a conventional Age-structured MODel, (AMOD) used in New Zealand snapper stock assessments (Gilbert et al.

2001), and CALEN. The CALEN model was fitted to data from the snapper fishery in the Hauraki Gulf/Bay of Plenty (Gilbert et al. this issue b), and we compare these estimates with an AMOD fit to the same data. AMOD uses age-specific approximations to account for what are most likely to be length-based processes such as partial recruitment of young age classes, fishing method selectivity, and mean weight at age (Gilbert et al. 2000). AMOD assumes growth is constant and deterministic and confirms to a von Bertalanffy length at age function. Therefore for the base runs of AMOD assume mean weight at age is constant over all fishing years. In CALEN length-based processes acting on each cohort are explicitly estimated. Since temperature effects on annual growth are accommodated, unlike AMOD, CALEN has the ability to vary mean weight at age between years.

Using a simulation approach, with CALEN as an operating model, the differences between AMOD and CALEN are evaluated in terms of bias and variance in model variables typically included in stock assessment advice. A full description of the CALEN and AMOD structure and error models is given by Gilbert et al. (this issue b) and Gilbert et al. (2000) respectively; only aspects relevant to the comparison of the two models are repeated here.

Hauraki Gulf/Bay of Plenty data

A description of the data input to CALEN is given in Gilbert et al. (this issue, b). A detailed description of the collection methods was provided for an assessment of the Hauraki Gulf/Bay of Plenty stock (Gilbert et al. 2000). The data used to compare the two models updates that of Gilbert et al. (2000) with additional annual catch weights, length and age samples, and CPUE indices for 2000 to 2001, and a 2001 research trawl survey.

The research and commercial fisheries data used to fit both models were derived either from projecting length samples through age-length keys, or from age samples. For AMOD, these data were expressed as proportions caught at age. For CALEN, they were expressed as a matrix of the proportions caught at age and length, with columns and rows being the age and length classes respectively.

Annual proportions at age and length data were available for four fisheries (longline, single trawl, Danish seine, and research trawl), for particular years from the period 1975 to 2001. In addition, four Danish seine catch-at-age samples (without length information) were available from the period 1970 to 1973. All ages were determined from readings of annual rings in otoliths. An "effective sample size" for a year's length and age data was determined using an arbitrary function of the number of commercial landings, the number of research trawl survey stations, the number of otoliths collected, and the number of methods to which the same age-length key was applied (Gilbert et al. this issue b).

Data from the research trawl surveys were used in the same way as for data from commercial fishing methods and input to CALEN as proportions caught at length and age. The research trawl survey data were not, however, input directly to AMOD. Instead these data were used to derive a time series of relative recruitment indices for input to AMOD (Gilbert et al. 2000). The series was made up of 11 survey estimates

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of 1+ y snapper relative abundance from the period 1983 to 1999. The data for other age classes were not used for input to AMOD.

Petersen mark-recapture experiments conducted in 1985 and 1994 provided estimates of absolute population length frequency that were input directly to CALEN. For use in AMOD, the Petersen abundance estimates were transformed using a length-weight relationship into estimates of absolute biomass (Gilbert et al. 2000).

A time series of longline catch per unit effort (CPUE) indices from 1990 to 2000 was input to both models.

A time series of Sea Surface Temperature (SST) measurements derived by Gilbert et al. (2000) for the period 1911 to 2001 was input to both models. The model SST series was an expansion of a series starting in 1967 of daily water temperature readings taken at the Leigh Marine Laboratory climate station. Gilbert et al. (2000) extended this series back to 1911 using a regression between the Leigh series and Auckland air temperature data.

Age-structured model (AMOD)

AMOD is similar to the stock synthesis model of Methot (1990). For a brief overview of the model structure see Appendix 1. Because the observed data used updates those used by Gilbert et al. (2000) for an earlier AMOD assessment the Hauraki Gulf/Bay of Plenty stock the AMOD estimates presented here differ from the results of Gilbert et al. (2000).

AMOD is discrete with respect to year; and the recruited population is divided into age classes 4 to 20 years, with the final age class being a plus group. The population is updated annually, with year-specific partial recruitments of age 4 and 5 year-old fish. The model assumes: both sexes have the same dynamics; constant natural mortality; a single stock with no spatial stratification; no age-specific fecundity; and no stock-recruit relationship. Annual fishing mortalities were age-specific, and calculated for five methods: longline, single trawl, Danish seine, other commercial (combined), and recreational. Constant weight at age was derived from von Bertalanffy, and length-weight parameters; thus the implicit assumption is that all fish of a given age have the same length and weight (Gilbert et al. 2000).

The population numbers at age in the model start year (1970) were assumed to represent an exploited equilibrium and calculated by assuming virgin recruitment and a constant F for years prior to 1970. The model was projected from 1970 to 2021. Annual relative recruitments from 1970 to 1979, and from 1997 to 2001 were determined from an estimated linear relationship between recruitment and SST, and relative recruitment indices from 1980 to 1996 were estimated as independent parameters. Fishing method selectivities at age were parameterized using double-normal distributions and estimated for the longline, single trawl, and Danish seine for the periods before and after the introduction of a quota-based fisheries management system in 1987. Constant selectivity at age of the other commercial and recreational methods was assumed. Annual gear-specific fishing mortality was determined from the observed catch weights and the separability assumption (Deriso et al. 1985) was made to distribute fishing mortality according to the year- and gear-specific

selectivity at age functions. A total of 37 parameters were estimated, comprising 17 annual recruitments, 18 selectivity at age parameters, and 2 pre 1970 total mortality parameters.

Parameters were estimated by a maximum likelihood fit (Fournier and Archibald 1982, Deriso et al. 1989), with terms for the CPUE abundance indices, catch-at-age, research trawl survey relative recruitment indices, and tag-recapture absolute biomass estimates. A lognormal error model was assumed for all four likelihood terms (Appendix 2). The model was fitted to observed catch-at-age for the age classes 5 to 20 years. Standard deviations on the log scale were assumed for the distributions (approximately equal to c.v.s on the natural scale), as follows: CPUE indices, $\sigma_{cpue,y} = 0.2$ for all y; catch-at-age, $\sigma_{C,y,g,a} = c \sqrt{n}$, (where c is the estimated sampling error, and n is the number of methods applied to a single age-length key in year y); research trawl survey relative recruitment indices, $\sigma_R^w = 0.3$, and tag-recapture absolute biomass, $\sigma_{B,y} = 0.4$ and 0.3 for y = 1985 and 1994 respectively.

Using the parameters from the model fit, equilibrium yield and stock biomass estimates were calculated. Virgin biomass (B_0) was the stock size under constant virgin recruitment, and zero fishing mortality.

Estimates of Maximum Sustainable Yield (MSY), and the biomass that supports MSY (B_{MSY}) were derived by optimising the model for yield per recruit ($F=F_{max}$). A hill climb search routine was used to find the optimum fishing mortality (F); constant virgin recruitment was assumed and gear selectivities and catch allocations were set to those of the year 2000.

Age- and length-structured model (CALEN)

CALEN is discrete with respect to age, length, and year, with the population described by an age and length state matrix that has a maximum length, and an aggregate age class for fish 30 years and older, i.e., plus groups, and is updated annually. Fish enter the matrix at age 0 y and all have the same length. Annual absolute recruitment is the product of a YCS index multiplied by virgin recruitment. YCS parameters were estimated either independently (for the years 1980 to 1996), or as a function of SST using an exponential relationship (for all other years to 2001).

The population numbers at age and length in the first year of model calculation, (1970), were calculated using the estimates of virgin recruitment, the SST-recruitment parameters, two prior fishing mortality parameters and mean growth. The population was projected from 1970 to 2001 accounting for additions from annual recruitment and growth, and removals from fishing (observed catches) and natural mortality (assumed constant).

Annual catch removals from CALEN's age-length matrix was calculated from an instantaneous, mid-year catch equation where method- and length-specific fishing mortalities were estimated for six fishing methods: longline, single trawl, Danish seine, other commercial (combined), research trawl, and recreational. Annual method-specific fishing mortality was determined from the observed catch weights, and the separability assumption (Deriso et al. 1985) was made to distribute annual fishing mortality according to the method-specific selectivity at length functions.

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Annual growth was modelled as a function of length. Fish in each length class were projected annually into the same or larger length classes according to parametric functions determining the size of the mean growth increment and its associated variance (Gilbert et al. this issue a). Variation in the mean growth increment between years was modelled by an annual multiplicative growth factor applied across all length classes. Thus, in a good growing year, all fish tended to grow faster, and conversely. The mean growth increment was also modified by an age-length factor with the effect that fish that have got ahead of the mean growth rate for their cohort continued to grow faster than equal sized but older fish, and conversely.

A total of 49 independent parameters were estimated by fitting the model to the four observed data types, (proportions caught at age and length, proportions caught at age, CPUE abundance index, and tag-recapture absolute length frequency estimates). These were: a SST-recruitment parameter; 17 annual recruitments; 10 parameters defining growth; 10 annual growth factors; a SST-growth parameter; 8 selectivity parameters; and 2 pre 1970 fishing mortality parameters defining the initial population state. Parameters were estimated using maximum likelihood. A Multinomial error structure was assumed for fitting to the proportions caught at age and length. Lognormal error structure was assumed for fitting the CPUE abundance indices, catch-at-age, and tag-recapture estimates of absolute length frequency (Appendix 2).

Using the parameters from the model fit, equilibrium yield and stock biomass estimates were calculated. Virgin biomass (B_0) was the stock size under constant virgin recruitment, zero fishing mortality, and mean growth. Optimising the model for yield per recruit to derive estimates for MSY and BMSY was done as described above for AMOD.

Model comparisons

CALEN and AMOD estimates of the population variables of interest derived from fits to the observed data were compared. These included: B_0 ; B_{MSY} ; annual biomasses (trajectory); biomass in 2001 and 2006 relative to B_{MSY} (B_{01}/B_{MSY} and B_{06}/B_{MSY} respectively); MSY; predicted surplus production in 2001 (CSP₀₁).

The sensitivity of the respective models to changes in their underlying structure was investigated in different ways. For AMOD, this involved replacing the constant assumed mean weights at age with observed estimates for the years available (1990 to 2001) derived from length and age samples from longline catches (Davies et al. in press). For CALEN the sensitivity cases chosen attempted to identify the structural components accounting for the differences between it and AMOD. This involved replacing the exponential growth function with a von Bertalanffy function, assuming constant mean growth, estimating a regime shift in selectivity at length before and after 1987 for the longline, single trawl and Danish seine methods; and lowering the maximum age and length classes. CALEN's sensitivity to reducing the relative weight of the CPUE and tag-recapture input data in the total negative log-likelihood was also tested.

Annual mean weights at age were calculated from the CALEN estimates of numbers at length and age from 1970 to 2001 using a length-weight relationship. These were compared to the constant mean weights at age assumed in AMOD that were derived from von Bertalanffy and length-weight parameters.

Conditional parametric bootstraps were performed using the CALEN model as the "true" model and the CALEN maximum likelihood estimate (MLE) fit to the observed data as the "true" parameters (Efron 1981). Pseudo-replicate sets of bootstrap data were generated conditioned on the CALEN MLE parameters, and the parameters were re-estimated by fitting both the CALEN and AMOD models to the bootstrap data. This was repeated 1000 times using a Cray T3E 1200 computer and FORTRAN90 for parallel processing.

The variability of the observation error structures estimated from the negative loglikelihood terms was used to describe the error distributions of the simulated observed data.

The proportion caught at age and length in the U^{th} bootstrap was simulated by approximating the multinomial with a modified binomial distribution,

$$C_{y,k,l,a}^{U} \sim B\left(p_{y,k,l,a}, \frac{V_{y,k}}{\left(\sigma_{AL}^{w}\right)^{2}}\right)$$

where $p_{y,k,l,a}$ is the MLE of the proportion caught at age *a* and length *l*, by method, *k*, in year, *y*, $C_{y,k,l,a}^{U}$ is the bootstrap number sampled , $v_{y,k}$ is the effective sample size and σ_{AL}^{w} is a c.v. weighting that produces a standard deviation of the Pearson residuals from the model fit equal to 1. Therefore,

$$p_{y,k,l,a}^{U} = \frac{C_{y,k,l,a}^{U}}{\sum_{l,a} C_{y,k,l,a}^{U}}$$

is the U^{th} simulated proportion at age *a* and length *l*, by method, *k*, in year, *y*.

The general formulation used for generating data for the Uth bootstrap from the lognormal observation error distribution for the catch-at-age, CPUE, and tag-recapture data sets was as follows,

$$\theta_i^U = \theta_i \exp\left(\mathcal{E}_i^U - \frac{(\sigma_i^*)^2}{2}\right)$$

where $\varepsilon_i^U \sim N(0, (\sigma_i^*)^2)$, θ_i is the MLE fit to the *i*th observation, and the standard deviation is,

$$\sigma_i^* = c. v_{\cdot i} \times \sigma_D^w$$

and where $c.v_i$ is the coefficient of variation of the i^{th} observation derived from the sample estimate and σ_D^{w} is a c.v. weighting for the D^{th} data set that produces a standard deviation of the Pearson residuals from the model fit equal to 1.

In the case of the tag-recapture absolute length frequency data a value of 1.0 was assumed for σ_D^w , as the data were considered too few to allow a satisfactory estimate of variability.

The procedure followed for summarizing the observed data for input to AMOD was repeated for each simulated data set. Proportions caught at age and length data were summed by length to produce proportions caught at age, and relative abundance indices of 2 year-old-fish were derived from the research trawl catch-at-age and length data. Tag-recapture absolute length frequencies were converted to absolute biomass using a length-weight relationship.

In each bootstrap, both models were projected over 20 years to 2021 assuming constant annual catch at the current management level, allocated between fishing methods according to the reported catches in 2000, with constant virgin recruitment.

In addition to the simulation comparisons, CALEN and AMOD were fitted to data generated by the CALEN MLE without observation error, and the fitted estimates of annual biomass from 1970 to 2001 were compared.

The relative bias, relative root mean squared error (RMSE), and relative deviations of the 5 and 95 percentiles were calculated for the CALEN and AMOD bootstrap estimates of the population variables of interest relative to the CALEN MLE "true" population variables. As listed above, the population variables (biomass and yield) were by definition all positive quantities.

$$Bias = \frac{\frac{1}{n} \sum_{U} \phi_{U,i}}{\frac{1}{TRUE} \phi_{i}} - 1$$

where ${}^{TRUE}\phi_i$ is the "true" population variable at the i^{th} location, and $\phi_{U,i}$ is the model estimate in the U^{th} bootstrap, and

$$RMSE = \sqrt{\frac{1}{n} \sum_{U} \left(\frac{\phi_{U,i}}{TRUE}\phi_i - 1\right)^2}$$

and

$$5\% Dev = \frac{5 \left\{\phi_i\right\}}{TRUE} - 1$$

$$95\% Dev = \frac{95 \left\{\phi_i\right\}}{TRUE} - 1$$

Results

The AMOD model fit closely resembled previous results (Gilbert et al. 2000), with the parameter estimates and objective functions changing little as a consequence of updating the input data to 2001. The model, on average, produced a good fit to the observed catch-at-age data. Catch-at-age residuals plotted against age show no systematic deviations, although there is a fairly wide spread in the residuals for the youngest age class included in the fit (5 years) (Fig. 1). With the exception of one very high observation in 1989, the predictions of the SST-recruitment relationship were reasonably consistent to the observed recruitment indices from research trawl surveys (Fig. 2). The AMOD predicted biomass for the tagging programmes although high, provide a reasonable fit to the tag-recapture absolute biomass estimates (Fig. 3), that is, the estimates lay within the relatively large measurement error bounds assumed for the observations (Gilbert et al. 2000). There is good consistency between AMOD mid-year biomass vulnerable to the longline method, and the observed relative abundance time series (Fig. 3).

The CALEN MLE also produced a reasonably good fit to the observed data (Gilbert et al. this issue b). The model fit diagnostics showed no unsatisfactory patterns in the proportions at age and length residuals or the residuals from the catch-at-age, tag-recapture length frequency and CPUE observations (Gilbert et al. this issue b).

CALEN MLE biomasses for years 1970 to 2001 are considerably lower than AMOD estimates, apart from a short period in the early 1990's where the two model biomass estimates coincide (Fig. 4). Both model biomass trajectories decline from 1970 to 1990. The models deviate widely after 1993; the AMOD biomass estimates increase rapidly while the trend in CALEN biomass is relatively flat. Although not fitted directly to the tag-recapture absolute biomass estimates, CALEN MLE estimates are closer to the tag-recapture estimates than the AMOD predictions.

CALEN MLE estimates of biomass from 1970 to 2001 were sensitive to structural assumptions similar to AMOD: fixing growth at a constant mean; using a von Bertalanffy function to define growth; changes to the selectivity at length (SEL86-87). The SEL86-87 model estimates were also sensitive to adjusting the error model by assigning lower relative weight to the CPUE and tag-recapture data (lowTG&CP). All the CALEN sensitivity runs gave trends in recent biomass similar that of AMOD, i.e., an upward trend since the early 1990's, and biomass in 2001 considerably higher than the CALEN MLE estimate (Figure 4a). CALEN biomass estimates were also sensitive to lowering the maximum aggregate age and length classes (lowA-Lmax), the effect being to further increase biomass after 1993 compared to the lowTG&CP run (Fig. 4b).

The AMOD biomass trajectory was more similar to the CALEN result when observed estimates of mean weight at age were used (Fig. 4b).

The AMOD and CALEN MLE estimates of the population variables of interest, B_0 , B_{MSY} , and MSY, are reasonably similar, and alter little in the sensitivity runs (Table 1). The CALEN MLE estimate of current stock status is less optimistic than AMOD, or any of the sensitivity runs, with biomass in 2001 predicted to be 49% below B_{MSY} . Similarly, CALEN CSP₀₁ estimates are considerably lower than the AMOD estimate although all model runs predict that the stock will rebuild over the next 5 years

The annual CALEN estimates of mean-weight-at-age differ considerably from the constant mean weights-at-age assumed for AMOD (Fig. 5). This is likely to be due to CALEN's ability to take into account variations in annual growth with the result that mean weight can have a wide range for any given age class (as much as 37% for 5 and 6-year-old fish, from 1970 to 2001). Mean weight at age is consistently higher in AMOD than CALEN for the ages between 7 and 25 years (Fig. 5). The assumed mean weight of the AMOD aggregate age class (20 years) is substantially lower than the mean weights for the age classes greater than 25 years estimated in CALEN, and is approximately 30% lower than the CALEN aggregate age class (Fig. 5).

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Mean weight at age as observed in commercial and research trawl catches has generally declined from 1985 to 2001, with a steep decline occurring from 1990 to 1995 (Fig. 6). Mean-weight-at age in the commercial catches appears to have remained low since 1993, but increases are evident in research trawl catches from 1998 to 2001. Although some of the between-year variability in the mean-weight-at-age observations for particular cohorts may be due to measurement error, (Millar et al. 1999), an overall trend is evident. The CALEN mean-weight-at-age estimates are broadly consistent with the observed trend; this consistent with the fact that the model fits well to the observed proportions caught at age and length over the period 1985 to 2001 (Gilbert et al. this issue b).

Compared to both the observed and CALEN weight at age estimates, the constant mean weight at age assumed in AMOD are lower for young age classes during the mid- and late-1980's, and are consistently and substantially higher during the 1990's, (Fig. 6). However, AMOD estimates are similar for the young age classes in 2001.

The AMOD fit to simulated observation data generated by the CALEN MLE without error, produces consistently higher biomass estimates, especially after 1993, compared to the MLE biomasses (Fig. 7). As would be expected the CALEN model estimates from a fit to the same simulated data set are identical to the MLE (Fig 7). The difference in biomass trajectories between AMOD and CALEN is similarly seen in the bootstrap results, with the means of AMOD annual biomass estimates from 1970 to 2001 being substantially higher than CALEN mean biomass, and "true" biomass (Fig. 8).

Differences seen between the AMOD and CALEN fits to the bootstrap data are generally similar to those described above for the AMOD and CALEN fits to the observed data. Both models predicted the declining trend in "true" biomass from 1970 to 1993, however AMOD biomass was consistently higher than CALEN by, on average, 50%. This difference between AMOD and "true" biomass increased to 177% in 2001. For both models, bootstrap mean biomass increased in the future, however, AMOD biomass was considerably higher, by 100% on average.

CALEN bootstrap confidence intervals were narrower than expected (Fig. 8). Although wider, AMOD confidence intervals were also relatively narrow. It is unlikely that these intervals portray all the uncertainty in the model estimates. Process error is ignored in both models. However, the results suggest lower uncertainty in CALEN biomass estimates compared to AMOD.

Mean bootstrap estimates of AMOD annual biomass and stock status in 2001 and 2006 were between 116% and 175% positively biased relative to the CALEN "true" population (Table 2). Mean bootstrap estimates for CALEN annual biomass showed negligible bias throughout the model calculation period, and relative RMSE for these estimates was less than 10%. The AMOD bootstrap confidence intervals considerably overestimated the "true" population annual biomass and stock status, indicated by the relative deviations of the 5 percentiles exceeding 1.0, i.e., the 5 percentiles of the AMOD bootstrap distributions were well above the "true" value.

AMOD estimates of B_0 , B_{MSY} , and MSY were relatively unbiased (between 0% and 15%) and the 5 to 95 percentile ranges of their bootstrap distributions were less than 20% of the "true" values. However, the CSP in 2001 predicted by AMOD was 50% positively biased, and even the 5 percentile was 23% positively biased (Table 2).

Discussion

Gilbert et al. (this issue b) showed by including parametric functions for annual variability in recruitment and growth the CALEN model fit to data from the Hauraki Gulf/Bay of Plenty snapper fishery was significantly improved. This variability could be partly explained by positive correlations with annual SST, although independently estimated growth and YCS factors deviated somewhat from the relationships. Using the same length and age data, although expressed in terms of proportions caught at age, AMOD provides a good fit to the observations. However, AMOD assumes constant growth and fixed mean weights at age.

The sensitivity tests revealed the large differences between CALEN and AMOD estimates of annual biomass from 1970 to 2001 could be attributed largely to differences in the structural model assumptions relating to growth, but also to fishing method selectivity functions, the maximum length and age, and the error model assumptions for the relative weight of input data in the objective function. Although biomass in 1970 was quite sensitive to the assumptions tested, it remained around 14 000 t lower than AMOD. This is probably due to the large difference in the mean weight at age for fish older than 20 years. Fish in these age classes were dominant in the population during the 1970's and early 1980's with the aggregate age class constituting 30% of the AMOD population biomass in 1970. The higher maximum weight at age of these fish, with continuous growth to 70 cm assumed in CALEN, enabled higher productivity in this population component. Consequently, under the CALEN growth model, a lower standing stock biomass in 1970, compared to the AMOD estimate, could sustain the same time series of catches.

CALEN estimates of annual biomass from 1993 to 2001 were considerably lower than AMOD due to the combined effects of the parametric functions for SST-dependence of growth and YCS. Long-term effects on a cohort's mean weight at age are caused by SST-dependent growth in the juvenile life stages of rapid growth. This creates "inertia" in the trend of mean fish weight in the population in subsequent years and has been observed for north Atlantic cod (Brander 2000). In a sense, average fish growth may be suppressed or enhanced in the first few years of life, and the effects of this period are largely retained throughout the cohort's existence. This directly affects population biomass, where relatively slight fluctuations in annual length increments throughout the population, translate to large fluctuations in mean weight, and hence population biomass. This is compounded by the impacts of YCS variation on recruited biomass that occur after a time lag caused by the time period required for individuals in a cohort to attain the size at recruitment. For snapper this is around 4 to 6 years (minimum legal size is 25 cm), and tends to be longer if winter SST is low. Consequently, CALEN predicts that sustained cold periods result in the delayed recruitment of smaller cohorts that have below average weight. In contrast, AMOD approximated delayed recruitment using a partial recruitment scalar, and assumed a higher constant weight at age during these periods, and therefore short-term predictions of recruited biomass were higher than for CALEN.

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Using data generated by CALEN, that included parametric functions describing this process, AMOD consistently overestimated the "true" population biomass, especially through the period immediately following the El Niño cycle in the early 1990's, despite the two models having similar YCS estimates. This indicates the importance of accounting for growth variability in the structural model, and shows the magnitude of positive bias (over 100%) in short-term predictions of biomass caused by constant mean weight and selectivity at age, in instances of sustained below average growth. Although not investigated in bootstraps with the chosen "true" population scenario, the converse is most likely true for periods of above average growth.

If the parametric functions estimated in CALEN are realistic in reflecting growth variability of fish populations such as snapper, the bootstrap results have significance both in terms of population modelling and management. It is suggested that structural model assumptions regarding growth variability be made with caution, and uncertainty estimation conditioned upon these assumptions should routinely be done as part of any stock assessment.

The impetus for the development of models like CALEN was for boreal populations with characteristically high growth variability (Guldbrandsen Frøysa et al. 2002). However, the CALEN model estimates predict that sustained periods of positive or negative deviations around mean growth and YCS have long-term impacts on population biomass for a temperate population, such as snapper. The significance of this for stock assessment and management of snapper may be realized given that SST trends in northeast New Zealand are largely determined by the El Niño Southern Oscillation (ENSO), (Bell and Goring 1998). During the 1991 to 1994 El Niño cycle, the sustained cold temperatures appear to have reduced growth rates, evident in observed mean weights at age, and produced poor YCS, and this was reflected in CALEN model estimates resulting in a substantial decline in predicted stock biomass. These predictions must be treated cautiously because CALEN estimates were sensitive to structural and error model assumptions regarding time-variant fishing method selectivity at length, model maximums for length and age, and the relative weights of input data in the likelihood. These aspects of the model require further investigation.

Considering the increasing awareness and evidence of growth variability in exploited fish stocks, and the range of possible mechanisms that have been advanced, this may be an essential feature in modelling fish stocks. Some advances in model development are now being made to address this need (Clark et al. 1999, Guldbrandsen Frøysa et al. 2002, Myers et al. 1997). Selectivity at length functions may be added to agestructured models with time-variant growth, thus modelling the effects of trends in observed mean weight at age (Clark et al. 1999). However, this approach derives new cohort length compositions in each year directly from the growth function, and so does not describe the cumulative effects of time-variant growth and length-specific mortality on each cohort's length composition through time. CALEN achieves this via the age-length matrix that is updated each year, and includes flexibility in the parametric growth functions that easily enables investigation of alternative growth model structures. There are two main approaches used in estimating uncertainty in fish population models, the bootstrap (frequentist) and Bayesian. The Bayesian approach has major advantages in situations of uninformative data, however, in situations using informative data, for which the probability distributions are well understood, the frequentist method may be well suited (Pattersen et al. 2001). We consider the matrix of proportion at length and age data input to CALEN to be highly informative with regards YCS and growth variability. This is indicated by the consistency in proportion at age between years for strong and weak year classes (Gilbert et al. 2000), and the clear trends in mean weight at age through time (Fig. 6). Detailed diagnostics of the residuals from the CALEN MLE fit to the observed data revealed no clear discrepancies with the parametric error distributions assumed (Gilbert et al. this issue b). Therefore, the distributions used to generate the pseudo-replicate data for the bootstraps are likely to have been suitable for investigating the performance of AMOD in the context set. However, the narrow bootstrap confidence intervals do not include uncertainty due to process error. Possible process error includes: incorrect historical catches (especially non-commercial), non-constancy of selectivity curves, non-constancy of natural mortality, deviations around the SST-recruitment relationship and systematic changes in mean recruitment over time. Process error is likely to have influenced both models similarly and therefore our results in terms of the direction and relative magnitude of estimator bias may be reasonable. However the conclusions possible regarding estimator variance are limited.

The choice of inference paradigm used in estimating uncertainty may depend upon the aspect of the model being investigated, and the context of the analysis (Pattersen et al. 2001). The purpose of the uncertainty analysis we present was to test the models conditioned upon structural model assumptions regarding growth variability specifically in the context of the Hauraki Gulf snapper stock. We applied the approach that is commonly employed, of using a best estimate to define a "true" population for simulations (Mohn 1993, Maunder 2001, Nielsen and Lewy 2002, Ianelli 2002). In the context of the snapper stock investigated, and given the structural model assumptions underpinning growth variability in the CALEN MLE, we conclude AMOD performs poorly in estimating stock biomass and status relative to B_{MSY}.

Acknowledgments

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Appendix 1: Age-structured model (AMOD)

Annual method-specific fishing mortality, $f_{y,k}$ for year y was multiplied by selectivity at age, $S_{k,a}$, to give instantaneous age-specific fishing mortalities,

$$F_{y,k,a} = f_{y,k} S_{k,a}$$
 1.1

where $f_{y,k}$ was estimated iteratively each year to make the model catch equal to the observed catch.

A double-normal function for selectivity at age, a, was used for each fishing method k,

$$S_{k,a} = \begin{cases} \exp\left(-\frac{1}{2}\left[\left(\frac{a - A \max_{k}}{\sigma_{k,left}}\right)^{2} - \left(\frac{8 - A \max_{k}}{\sigma_{k}'}\right)^{2}\right] & a \le A \max_{k} \\ \exp\left(-\frac{1}{2}\left[\left(\frac{a - A \max_{k}}{\sigma_{k,right}}\right)^{2} - \left(\frac{8 - A \max_{k}}{\sigma_{k}'}\right)^{2}\right] & a > A \max_{k} \end{cases}$$

$$1.2$$

where $\sigma'_{k} = \sigma_{k,left}$ if $Amax_{k} \ge 8$ and $\sigma'_{k} = \sigma_{k,right}$ if $Amax_{k} < 8$.

Catch-at-age was calculated after Deriso et al. (1989):

$$C_{y,k,a} = \frac{F_{y,k,a}}{\sum_{k=1}^{5} F_{y,k,a} + M} \left[1 - \exp\left(-\sum_{k=1}^{5} F_{y,k,a} - M\right) \right] N_{y,a}$$
 1.3

and population numbers at age at the beginning of the following year were calculated:

$$N_{y+1,a+1} = N_{y,a} \exp\left(-\sum_{k=1}^{5} F_{y,k,a} - M\right)$$
 1.4

and for the aggregate class:

$$N_{y+1,20} = N_{y,20} \exp\left(-\sum_{k=1}^{5} F_{y,k,20} - M\right) + N_{y,19} \exp\left(-\sum_{k=1}^{5} F_{y,k,19} - M\right)$$
 1.5

where $N_{y,a}$ is the population number at age, *a*, at the beginning of year *y*.

The initial population conditions in the first year of model calculation (1970) were defined by two total mortality parameters Z_1 and Z_2 and a SST-recruitment relationship. The numbers at age in the population was,

$$N_a = Rr_{1970-a}e^{-aZ} 1.6$$

where R is virgin recruitment, r_{1970-a} is the relative strength of year class 1970-a and for age classes younger or older than 20 years Z_1 or Z_2 is used respectively. YCS indices not estimated as independent parameters were derived from a relationship with SST,

$$r_{y} = e^{\alpha + \beta T_{y}}$$
 1.7

where T_y is the SST in year y.

Population biomass was calculated using mean weight at age estimated using the von Bertalanffy growth parameters and length-weight parameters,

$$w_a = c(l_*^b) \tag{1.8}$$

where c = 0.04467 and b = 2.793 (Paul 1976) and l_a is the mean length at age a. Annual biomass for the recruited population (ages 4 years and older) is therefore

$$B_{y} = \sum_{a=4}^{20} N_{y,a} w_{a}$$
 1.9

Appendix 2: Maximum likelihood estimates

Model parameters were estimated by maximum likelihood using a FORTRAN downhill simplex minimising procedure (Press *et al.* 1992) and the terms of the objective function were as follows.

Multinomial error model: the negative log-likelihood (less constant terms) for a year's proportion at age and length sample was

$$\Lambda = -\sum_{k,l,a} v_k \times {}^{OBS} p_{k,l,a} \times \log p_{k,l,a} \qquad 2.1$$

where ${}^{OBS} p_{k,l,a}$ and $p_{k,l,a}$ are the *i*th observed and expected proportions at age *a* and length *l* respectively by method *k*, v_k is the effective sample size, and σ_{AL}^{w} is the c.v. weighting for proportion at age and length data as described in the text.

Log-normal error model: each negative log-likelihood term was,

$$\Lambda = \sum_{i} \log(\sigma_{D,i}) + \frac{1}{2} \sum_{i} \left(\frac{\log({}^{OBS}\theta_{D,i}) - \log(\theta_{D,i}) + \frac{(\sigma_{D,i})^2}{2}}{\sigma_{D,i}} \right)^2 \qquad 2.2$$

where ${}^{OBS}\theta_{D,i}$ and $\theta_{D,i}$ are the *i*th observed and expected variables respectively for data type D, $\sigma_{D,i}$ is the standard deviation of the the *i*th variable. In AMOD all the expected variables (CPUE, catch-at-age, research trawl relative recruitment indices, and tag-recapture estimates of absolute biomass) were substituted into equation 2.2; and in CALEN these were CPUE, catch-at-age, and tag-recapture estimates of absolute length frequency. The CALEN expected variables are described by Gilbert *et al.* (this issue b). For AMOD the expected relative abundance indices for the CPUE likelihood were derived using mid-year model biomass vulnerable to the method k' =longline,

$$I_{y} = q B_{y,k'}^{mid}$$
 2.3

where for AMOD

$$B_{y,k'}^{mid} = \sum_{a=4}^{20} S_{k',a} N_{y,a} \exp\left(-\frac{1}{2} \sum_{k=1}^{5} F_{y,k,a} - \frac{1}{2} M\right) w_a^{mid}$$
 2.4

and w_a^{mid} is the mid-year weight at age taken from an adjusted von Bertalanffy growth equation, and the catchability coefficient, q is estimated analytically,

$$q = \exp\left(\frac{1}{\sum_{y} \frac{1}{\sigma_{cpue,y}^{2}}} \left(\sum_{y} \frac{\left(\log^{OBS} I_{y} - \log I_{y}\right)^{2}}{\sigma_{cpue,y}^{2}}\right)\right)$$
2.5

The AMOD expected variable for the proportions caught at age a, by gear, g, in year, y, is,

$$\rho_{y,g,a} = \frac{C_{y,g,a}}{\sum_{a=4}^{20} C_{y,g,a}}$$
2.6

where $C_{y,g,a}$ is the model estimate of numbers caught at age from equation 1.3. The AMOD expected variable for trawl survey relative recruitment index was r_y , and for the tag-recapture estimates of absolute biomass was B_y .



Fig. 1. Scatterplot of standardised residuals from the AMOD fit to the catch-at-age time series with respect to fish age, showing mean of residuals at age (solid line).



Fig. 2. Annual relative recruitment indices predicted from AMOD versus observed relative recruitment indices from research trawl surveys, with the solid line showing a log-linear relationship between recruitment (abundance of 1+-year-olds) and sea surface temperature.



Fig. 3. AMOD start-year biomass (Biomass) fitted to absolute abundance estimates from tag-recapture studies (Btag), and AMOD mid-year biomass vulnerable to the longline method (Bmid) fitted to longline relative abundance (Bcpue).



Fig. 4. Comparison of annual biomass estimates from CALEN and AMOD fitted to observed data, with sensitivity tests of CALEN to low relative weight of tag-recapture data and CPUE indices (LowTG&CP), and a regime shift in selectivity at length (SEL86-87), (a.); and CALEN sensitivity to lower maximums for age and length (lowA-Lmax), and AMOD sensitivity to assumed mean weight at age derived from observations (ObsWta), (b.). Btag is the tag-recapture estimate of absolute biomass.

Table 1. Biomass and yield estimates from CALEN and AMOD models, with a sensitivity to using observed mean weights at age in AMOD (ObsWta), and CALEN sensitivities by subsequently including low relative weight of tag-recapture data and CPUE indices (LowTG&CP), then adding a regime shift in selectivity at length (SEL86–87), and then lowering the maximum age and length classes (lowA-Lmax). Model variables are biomass in 2000, 2001 and virgin (B₀₀, B₀₁, and B₀ respectively), biomass in 2006 from a deterministic projection under constant virgin recruitment and current catch levels (B₀₆), maximum sustainable yield (MSY), and equilibrium biomass that supports MSY (B_{MSY} as defined in the text), and predicted current surplus production in 2001 (CSP₀₁). All biomass and yields are x1000 t.

	\mathbf{B}_{0}	B _{MSY}	B ₀₀	\mathbf{B}_{01}	B_{01}/B_{MSY}	B_{06}/B_{MSY}	CSP ₀₁	MSY
AMOD	280.7	64.7	50.3	54.9	0.85	1.21	9.0	8.0
ObsWta	281.5	65.2	43.3	45.8	0.70	1.11	12.6	8.1
CALEN	305.2	60.9	29.6	31.0	0.51	0.76	7.0	7.3
SEL86-87	293.4	62.6	42.1	43.2	0.69	0.86	5.9	7.2
lowTG&C	P 294.9	62.0	49.2	50.8	0.82	1.01	6.2	7.3
lowA-Lma	x 308.7	67.7	56.2	58.1	0.86	1.06	6.6	7.6






Fig. 6. Estimates of mean weights at age of snapper as observed in samples (OBS) from longline and research trawl catches (LL and RT respectively), and from CALEN (solid line), and that assumed in AMOD (dashed line), for the available years sampled, and for selected age classes.



Fig. 7. Biomass estimates from CALEN and AMOD models fitted to "observed" data generated by the CALEN maximum likelihood estimate model without error.



Fig. 8. CALEN and AMOD bootstrap mean estimates of the "TRUE" population biomass, and 90% confidence intervals from 1970 to 2001, with projections with stochastic recruitment to 2021.

Table 2. Variables from the CALEN maximum likelihood estimate (MLE) defining the "TRUE" population, compared with the bootstrap mean estimates of AMOD and CALEN, with the relative bias, relative root mean squared error (RMSE), and deviations from the 5 and 95 percentiles (5% ile and 95% ile Deviation) of the bootstrap distributions relative to CALEN MLE. Variables include biomass in 2001, 2006, virgin biomass (B₀₁, B₀₆, and B₀ respectively), maximum sustainable yield (MSY), equilibrium biomass that supports MSY (B_{MSY}), stock status in 2001 and 2006 relative to B_{MSY} (B₀₁/B_{MSY}, B₀₆/B_{MSY}), and predicted current surplus production in 2001 (CSP₀₁).

	B ₀	B_{MSY}	B ₀₁	B ₀₆	B_{01}/B_{MSY}	B_{06}/B_{MSY}	CSP_{01}	MSY
CALEN MLE	305.161	60.944	30.998	46.085	0.509	0.756	6975	7340
AMOD Mean	303.958	68.586	85.184	112.598	1.240	1.638	10335	8413
CALEN Mean	308.245	61.921	30.801	46.268	0.497	0.747	7051	7405
Relative Bias								
AMOD	-0.004	0.125	1.748	1.443	1,438	1.167	0.482	0.146
CALEN	0.010	0.016	-0.006	0.004	-0.022	-0.012	0.011	0.009
Relative								
RMSE								
AMOD	0.048	0.136	1.793	1.477	1.468	1.186	0.511	0.155
CALEN	0.020	0.025	0.089	0.077	0.084	0.068	0.060	0.016
5%ile Deviation								
AMOD	-0.067	0.053	1.221	1.004	1.035	0.863	0.225	0.079
							-	-
CALEN	-0.018	-0.013	-0.149	-0.125	-0.154	-0.125	0.083	0.012
050/ile Devietie								
95%ile Deviatio	<u></u>							
AMOD	0.088	0.228	2.529	1.990	1.990	1.566	0.785	0.247
CALEN	0.039	0.047	0.138	0.129	0.114	0.095	0.112	0.030